Motor preparatory processes recorded in the leg of man

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Publication date:
1987

Document Version
Publisher's PDF, also known as Version of record

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J.G.M. SCHEIRS

MOTOR PREPARATORY PROCESSES RECORDED IN THE LEG OF MAN

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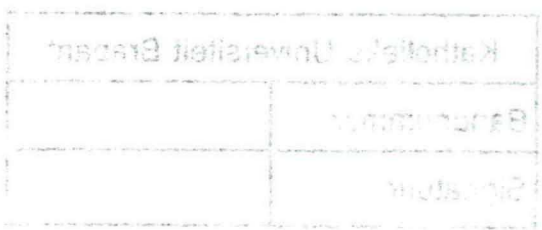
Proefschrift
ter verkrijging van de graad van doctor
aan de Katholieke Universiteit Brabant,
op gezag van de rector magnificus, prof. dr. R.A. de Moor,
in het openbaar te verdedigen ten overstaan van
een door het college van decanen aangewezen commissie
in de aula van de Universiteit
op vrijdag 12 juni 1987 te 14.15 uur

door

Johannes Gerardus Maria Scheirs

geboren te Hilvarenbeek.

Promotor: Prof. dr. C.H.M. Brunia



printed by ELKA bv Tilburg, The Netherlands

Nu myn lichaem wort op veelerley wijs nae mijn wil ende goetduncken bewogen: want mijne tonge, so ik maer spreeken wil, slingert wonderlijk in mijnen mondt gins en weer: mijn armen, so ik in 't water lich en swemmen wil, die recken en plonsen; mijn voeten, so ik op het landt ben ende gaen wil, die worden dan den eenen dan den anderen voor my henen geworpen. Edoch al wederom dit bewegen en beroeren en is mijn doen niet: Ick en wete niet, hoe het geschiede: Onbeschaemt most ik wesen, een houten backhuys (gelijk men seght) most ik hebben: woude ik seggen dat ik dee, het ghene ik niet en weet hoe het gedaen wort: Ik en wete niet hoe ende op wat wijs, ick en weet niet door wat zenuen, peesen of andere gaten, de beweging uyt mijn hersens in mijn spieren ende ledemaeten invloeyt: ick en weet niet, hoe de bewegingh tot de hersens ghenaekt: ick en weet niet of s' er al ghenaekt, of s' er al genaeken moet om van daer in de andere deelen mijnes lichaems af te sijpen;..... het sal jaeren en daegen aen loopen, eer ik mijn wercktuychjen, dat ik toch alle gebruyken most om een woordeken uyt den mondt te geven, wel ter deech oversien sal hebben.

(Arnout Geulincx, Van de Hooft-Deuchden, 1667)

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Appendices

Acknowledgements

The research upon which this thesis is based was carried out at the Katholieke Universiteit Brabant during the years 1979-1985. Many people provided practical help, advice or encouragement. These were the members of the vakgroep Fysiologie en Fysiologische Psychologie, the Electronische afdeling, Hout- en Metaalafdeling and Automatiseringsafdeling of the Instrumentele Dienst and the members of the Audio-Visuele Centrum.

Two of the people included above deserve special mention: Professor Cees Brunia who made the research possible, and Stephan Haagh for his willingness to participate in the solving of problems, both practical and theoretical and at whatever moment they occurred.

Financial support was provided by the Dutch Organisation for Basic Research (ZWO) (1979-1982), the Katholieke Universiteit Brabant (KUB) (1983) and the Tilburg Institute for Advanced Studies (TIAS) (1984-1985).

FIGURES:

The figure on the cover (concept of the reflex arc) is from R. Descartes, Le monde; Traité de l'homme, 1664. Reprinted in: C. Adam and P. Tannery, Oeuvres de Descartes, Paris, Librairie philosophique J. Vrin, 1974.

The figure on page 87 (alpha motoneuron) is after B. Kolb and I.Q. Whishaw, Fundamentals of human neuropsychology, New York, Freeman, 1985.

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APPENDICES:

Appendix 1 has been published in Psychophysiology, 1982, 19, 63-70. The article was authored by C.H.M. Brunia, J.G.M. Scheirs and S.A.V.M. Haagh and is reprinted here by permission from The Society for Psychophysiological Research, Inc.

Appendix 2 has been published in Physiology and Behavior, 1982, 28, 681-685. The article was authored by J.G.M. Scheirs and C.H.M. Brunia and is reprinted here by permission from Pergamon Journals Ltd.

Appendix 3 has been published in The Journal of Motor Behavior, 1985, 17, 96-109. The article was authored by J.G.M. Scheirs and C.H.M. Brunia and is reprinted here by permission from Heldref Publications.

Appendix 4 has been published in Biological Psychology, 1986, 23, 163-178. The article was authored by J.G.M. Scheirs and C.H.M. Brunia and is reprinted here by permission from North-Holland publishing Company Inc.

Chapter I.

Introduction

I. INTRODUCTION

1. Reflex action

The living organism is characterized by its continuous responding to stimuli in the outside world. The fastest way of doing so is by means of a reflex. The withdrawal of an arm caused by the touching of a hot stove, for instance, takes less time than voluntarily touching an object upon command.

The concept of reflex action, that is that part of our behavior is not voluntary but automatic, must have been known long before the era of scientific investigations. Greek philosophers and physicians, like Aristotle and Galen, mentioned the distinction between the two types of behavior in their writings (Fearing 1970). However, extended attention was first paid to reflex behavior by René Descartes in the early 17th century (Brazier 1983). Descartes did not use the word reflex as such, but proposed that it is not necessary for the soul to take part in all our actions. The word reflex, or "motus reflexus" as used by Thomas Willis (Van den Berg 1973), was only introduced in scientific language in the late 17th century and gained general acceptance in the century thereafter.

Yet, despite the fact that the reflex is fast, apparently simple, reproducible and purposeful and thus has intrigued many, much about what constitutes reflex action and how it is accomplished is still unknown.

The present day concept of the reflex covers a broad range of meanings. In the behavioral sciences, the word has often been used in a descriptive sense, to refer to basic units in human behavior. Among these are innate responses which come to be elicited by previously neutral stimuli on the basis of learning (Pavlov 1927). Among them are also complex reactions which involve changes in several physiological systems and which are readily evoked by several kinds of stimuli characterized by some global features, such as newness, meaning or a high intensity; these are the orienting or defensive reflexes described by Sokolov (1963). The word reflex is also used to designate voluntary motor acts that have become highly automatized as a result of training. For instance, the immediate activating of the brakes by a cardriver who perceives an obstacle is often called reflex behavior.

A common factor in these meanings of the word seems to be the integration of sensory and motor systems in a highly preconceived way, which results in speed and a rather stereotyped

behavioral pattern.

In physiology, the emphasis has been on the anatomical prerequisite of this sensory-motor integration: the reflex arc. The reflex arc comprises a receptor cell, a conductive system (an afferent and an efferent limb) and, eventually, an effector organ (muscle or gland). On the basis of this, a classification of reflexes can be made according to the particular stimulus, the typical behavioral response, the receptor, the anatomical structure or the number of synapses that is involved.

2. Tendon reflexes

One particular reflex, the reflex that is used throughout the present study, is the Achilles tendon reflex or tendon jerk. The reflex is variously described as being myotatic, segmental, spinal and monosynaptic. Myotatic as the effective stimulus is muscle stretch (Lidell and Sherrington 1924). Segmental and spinal as the transmission of information in the reflex arc is thought to take place within one segment of the spinal cord. The reflex is also primarily monosynaptic as argued by Lloyd (1943a), although di- and trisynaptic pathways might also be involved (Burke, Gandevia and McKeon 1984).

The Achilles tendon reflex and the patellar reflex or kneejerk belong to the same class of reflexes. Both are well known because of their use in clinical diagnosis. Tendon reflexes, however, were not described until 1875, after Erb (1875) and Westphal (1875) had observed the kneejerk in some of their patients and had at first mistaken it as a sign of pathology.

Soon after this discovery, a large amount of research was carried out aimed at demonstrating the principles of facilitation and inhibition in the kneejerk. At first, emphasis was on the effects of stimulation of peripheral nerves and skin (Mitchell and Lewis 1886), and on motor activity in remote parts of the body (Jendrassik 1883), which were both found to reinforce the reflex.

3. Tendon reflexes and psychological functioning

Even to the early investigators, who were primarily concerned with modification of the kneejerk by physiological factors, the enormous variability of the tendon reflexes appeared impressive. Lombard (1887) stated that factors such as rest,

nourishment, invigorating weather and voluntary movements increased the average knee-jerk. He also made explicit reference to the influence of psychological factors on reflex excitability, by concluding that hearing a baby cry in the next room acted as a reinforcement, whereas loud sounds, if devoid of interest, had no appreciable effect. In sum, almost every form of mental activity was reported to have a facilitating effect upon the kneejerk.

Bowditch and Warren (1890), in an early investigation on the effects of auditory and visual stimulation, observed the complete disappearance of the kneejerk during sleep. In describing the course of their longlasting experiments they stated: "the tendency to sleep was sometimes quite irresistible, and in eight or nine cases the experiment was continued after the subject had yielded to it and was sleeping soundly. It was then found that the knee-jerks, both normal and reinforced, grew gradually smaller, and, when sleep was profound, disappeared entirely, the blow upon the knee being absolutely without effect". These authors concluded that "the variations in the mental state of the subjects of the experiments...were quite sufficient to cause the differences which were observed in successive knee-jerks under apparently identical conditions" and that, therefore, "great caution would appear to be required in establishing any conclusions about the influence of disease upon the same phenomenon".

These early and inadvertent observations led to experiments in which the effects of mental tasks on the tendon reflex were the prime subject of investigation. Tuttle (1924) recorded the amplitude of the kneejerk (as assessed by actual movement of the leg) during a "passive" condition which required no attention, and during mental work, i.e. arithmetic, conversation or mental testing. All subjects showed increased reflexes during mental work. The kneejerk was the reflex that was most frequently investigated at that time. The Achilles tendon reflex received attention only in a minority of cases (e.g. Tuttle, Travis and Hunter 1927).

These early reports make clear, that at the turn of the last century it was recognized that the great variability of the tendon reflexes might indicate that they were sensitive indicators of mental functioning.

4. The Achilles tendon reflex: its use in reaction time studies

The Achilles tendon (T-) reflex was first employed in psychological experiments by Paillard (1955). These investigations were technically more advanced than before, since stimulation parameters were better controlled and since measuring reflex amplitudes was done by means of electromyography (EMG), rather than by recordings of kinematic parameters. Paillard's aim was to elucidate the neurophysiological mechanisms behind the tendon reflex enhancement, that had so often been found during mental tasks. For that reason he employed two types of reflexes that could be elicited in the human calf muscles: the T-reflex and the so called Hoffmann (H-) reflex, which was considered as the electrical counterpart of the T-reflex (Magladery and McDougal 1950).

According to Paillard, testing the activity in neuronal circuits by means of reflexes had some important advantages as compared to the recording of spontaneous EMG activity. He argued that reflexes could detect neuronal changes which are subliminal, i.e. which are unable to discharge motoneurons and furthermore, that reflexes could show inhibitory influences on the motoneuron pool in the absence of EMG activity. These arguments in favor of the reflex technique were summarized as follows: "La richesse des indications fournis par une exploration systématique des réflexes tendineux a cadences rapides, comparativement aux indications assez imprécises, difficilement analysables, fournies par l'enregistrement direct ou même "integré" des electromyogrammes, apparait de façon frappante..." (Paillard 1955).
In his study Paillard (1955) described the modification of the T-reflex not only during sleep and mental arithmetic, but also during a standardized behaviorial procedure that is now generally referred to as a warned reaction time task. In such a task, subjects receive a stimulus that serves as a warning for a second stimulus which is to appear after a short delay. Delays can be a few seconds or less. The subject's task is to respond as fast as possible to the second (imperative) stimulus. In the interstimulus-interval or foreperiod, preparatory processes take place which facilitate performance.

During the past two decades, numerous investigators have employed this technique and have extended the design proposed by Paillard, but they failed to obtain consistent findings. Preparation for a motor response was variously found to affect H- and T-reflexes differentially or in a comparable way, to show either selective or generalized effects and to cause reflexes to increase or to decrease (Requin 1967, 1969; Coquery 1969;

Gerilovski and Tsekov 1971; Brunia and Vuister 1979; Bonnet 1981).

There were, however, great differences in experimental procedures, which might have contributed to these discrepancies. The length of the foreperiod and the positioning of the electrodes over either the soleus or the gastrocnemius muscle, for instance, are known to be important factors (Semjen, Bonnet and Requin 1973; Woollacott, Bonnet and Yabe 1982). Furthermore, unusual methods of calculating standardized scores have been employed in some experiments for instance by Requin, Bonnet and Semjen (1977), as will be illustrated later. Finally, the degree of facilitation and inhibition of the H-reflex was found to depend on the amplitude of the control reflex (Meinck 1980).

In the experiments to be described in this thesis, reaction time studies were again conducted to elucidate the way in which the central nervous system (CNS) processes information and channels down the neural commands to the muscles in order to produce movement. When a movement is to be executed the flow of information starts in the brain, or in the senses if the movement is triggered externally, and ends in the muscles. Our interest has been focussed on the ultimate neural level at which this stream of information can be modified: the spinal cord.

It has recently been argued that cortical activity, even when resulting in the discharge of some alpha motoneurones, is often not easily detected in the EMG (Evarts and Fromm 1980). Therefore, reflexes can be used as a tool, to reveal aspects of the motor preparatory process that might otherwise remain undetected. We choose to employ the T-reflex throughout this study, as its evocation was found to be less intrusive to the subjects than the electrically evoked H-reflex and second, as in direct comparisons of both reflexes the T-reflex appeared to be more sensitive than or as sensitive as the H-reflex to psychological functioning (Paillard 1955, 1959; Bathien and Hugelin 1969; Brunia 1971). In studying the time course of preparation, 4 second foreperiods were used. The choice of these long foreperiods, instead of the more common foreperiod length of 1 second or less, was based on recent slow cortical potential studies showing that processes relating to stimulus processing and others relating to movement execution might overlap during short foreperiods (e.g. Rohrbaugh, Syndulko and Lindsley 1976).

In the next chapter, we will briefly review the anatomy of the T-reflex and the ways reflex amplitude can be modulated by neural commands. Afterwards, some features of the motor preparatory process will be described, as well as the patterns of change in various physiological parameters during warned reaction

time tasks. Finally, the two lines of argument will be combined in a description of and a discussion about the four experiments that constitute this thesis.

Chapter II.

Physiological mechanisms of reflex modification

II. PHYSIOLOGICAL MECHANISMS OF REFLEX MODIFICATION

1. Reflex Anatomy

The first component of the reflex arc is the receptor cell. Throughout the muscles, skin and joints, there are several types of sensory organs that signal peripheral changes to the CNS. The ones that are of prime importance in establishing a mechanically evoked reflex response, however, seem to be the mechanoreceptors in the muscle. These are the Golgi tendon organs and the muscle spindles.

The tendon organs, located near the junctions of muscle and tendon, have large afferent connections (group Ib fibers) with the spinal cord. They have a low excitation threshold. Tendon organs may be considered contraction receptors, as they have a low sensitivity to large dynamic stimuli but instead provide the CNS with a continuous averaged measure of muscle tension (Matthews 1981).

The muscle spindles, embedded in the muscle, are sensitive primarily to changes in muscle length. The role of these particular receptors in reflex control can hardly be overemphasized, since the effective stimulus in case of a tendon reflex is muscle stretch. The spindle is composed of fibers which run in parallel to the (extrafusal) muscle fibers and which have contractile properties. Because of this arrangement, muscle contraction and release as well as passive lengthening will be reflected by changes in spindle output.

The spindle fibers, which are called intrafusal fibers, can be divided in two types, the distinction being made on morphological grounds: nuclear bag and nuclear chain fibers. On the intrafusal fibers, both bag and chain, lie the sense organs, which are designated as the primary or annulospiral and the secondary or flowerspray endings. This distinction is made according to the size and conduction velocity of the fibers innervating the endings: the afferent fibers that innervate the primary endings (group Ia fibers) are thicker and have a faster conduction velocity than the fibers that innervate the secondary endings (group II fibers). The secondary endings lie predominantly on the chain fibers, the primary endings on both chain and bag fibers. Fig.1 presents a simplified view of the major fibers and connections in the muscle spindle.

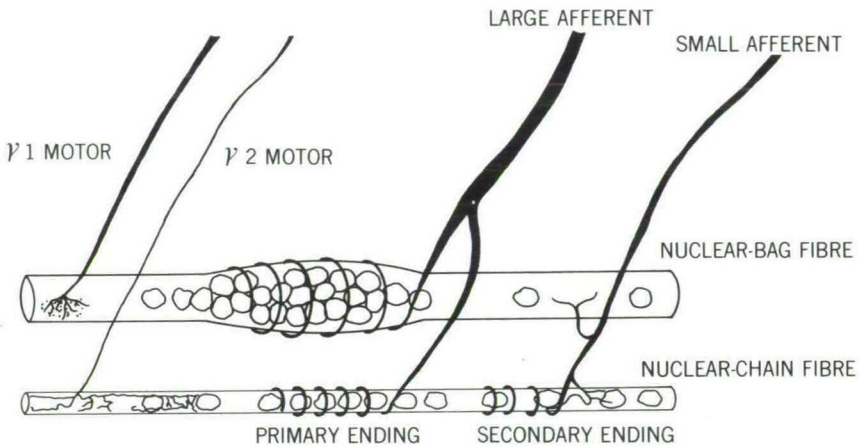

Fig. 1 Simplified diagram of the central part of the human muscle spindle.
The diagram shows only one nuclear bag and one nuclear chain fiber. The primary sensory endings are innervated by large (group Ia) fibers, and the secondary endings by relatively small (group II) fibers.
The gamma-1 and gamma-2 neurons serve a motor function; the two types of efferent fibers, however, are not functionally but only morphologically distinct (after Matthews 1981).

There is a functional distinction between the primary and secondary endings that is relevant to our work. It has been found that the change in firing of the primary endings when movement starts or stops is much greater than that of the secondary endings. So the primary endings have the greatest sensitivity to stimuli that change the length of the spindle (Matthews 1981). While the secondary endings provide a signal that chiefly indicates the instantaneous value of muscle length, the primary endings seem to combine information relating to length and the velocity of stretching (and possibly the acceleration). Now it is conceivable that when the Achilles tendon is tapped, both the extrafusal and intrafusal fibers of the soleus muscle are stretched. The increase in length is signalled by the primary endings and an afferent volley is caused to travel along the large Ia fibers to the L5 and S1 segments of the spinal cord. In

the spinal cord, there is a chiefly monosynaptic connection to the alpha motoneurons of the receptor bearing muscle. The activity in these motoneurons causes extrafusal fibers of the soleus muscle to contract in a highly synchronous manner (see Fig.3).

Accumulating evidence has shown that the question as to which alpha motoneurons fire when there is an excitatory input to the motoneuron pool, can be answered by referring to the so-called size principle (e.g. Henneman, Somjen and Carpenter 1965). This notion implies that during contraction motoneurons are not recruited randomly but in order of increasing size. It has been shown that this general principle of size related recruitment is also active in reflex contractions (Bawa, Binder, Ruenzel and Henneman 1984).

When the foot is free to move, the synchronous activation of muscle fibers results in a brisk extension (plantar flexion) of the foot. In the surface EMG, the reflex becomes visible as a triphasic compound action potential with a short latency (see Fig.2). The latency of the reflex, that is, the time between the application of muscle stretch and the resulting reflex potential in the EMG, is about 30 to 40 msec. This latency depends primarily on transmission time in the afferent and efferent limbs of the reflex circuit and appears to be rather constant within subjects.

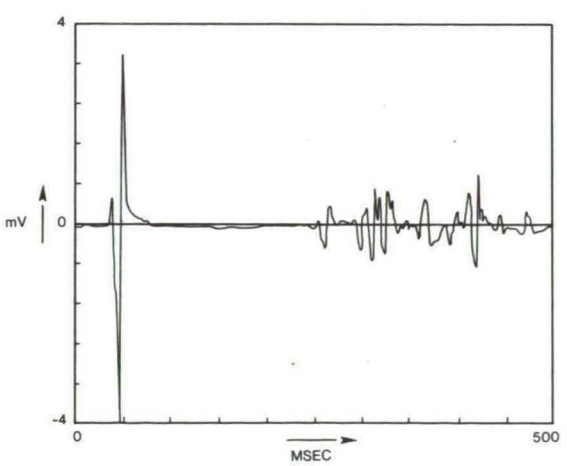

Fig. 2 Achilles tendon reflex trace (triphasic potential) as it appears in surface EMG recordings.
The tendon tap is applied at time zero. The reflex potential is followed by a voluntary muscle contraction (asynchronous activity at the right).

With regard to the last component of the reflex arc, the muscle, it is often customary to speak of the triceps surae instead of the soleus muscle. This is done since in case of a tendon tap the soleus muscle is not stretched exclusively, but muscle spindles in the gastrocnemius muscle are activated as well. Furthermore, experiments with cats have shown that there are ample monosynaptic connections between Ia afferents and motoneurons of synergist and even unrelated muscles (Eccles, Eccles and Lundberg 1957). Despite this, the homonymous connections between spindle afferents and motoneurons seem to be more effective in the soleus than in the gastrocnemius muscle (Mao, Ashby, Wang and McCrea 1984). The soleus muscle appears to be most relevant in case of a T-reflex, therefore.

2. The locus of facilitatory and inhibitory influences in the spinal cord

Of special importance is the fact that the muscle spindle's sensitivity to stretch is not fixed but can be modified. This is accomplished by small diameter motor neurons (called fusimotor neurons or gamma-efferents) and, presumably, by beta-axons, branches from the alpha motoneurons that innervate the extrafusal fibers (Post, Rymer and Hasan 1980) (see Fig.1).

So besides sensory endings on the chain and bag fibers, there are motor endings which are called plate and trail endings. The fusimotor fibers are, again, subdivided. According to a difference in function there exist dynamic and static fusimotor axons. The dynamic axons, when stimulated, sensitize the primary sensory endings to subsequent stretch and release. These axons seem to innervate a subcategory of bag fibers (called type bag-1). Static axons, innervating bag-2 and chain fibers, tend to diminish this increased responsiveness and make the primary ending function more like the secondary ending.

An effective mechanism for the CNS to modify the reflex response, therefore, would consist of adjusting the primary ending's sensitivity to stretch by activating or inhibiting the dynamic fusimotor neurons. Such a mechanism of reflex modification, incorporating a supraspinal drive selectively influencing the gamma-motor system, was proposed by Paillard (1955) and by Brunia (1971). It was suggested by these authors and more recently by Enoka, Hutton and Eldred (1980) and by Bonnet, Requin and Semjen (1981), that the level of fusimotor drive was reflected in the difference between the H- and T-reflex time course.

Apart from the fact that assessing fusimotor drive from comparing H- and T-reflex changes is probably invalid (Burke, Gandevia and McKeon 1983), there are strong indications that during muscle contraction there exists a coactivation of extra- and intrafusal muscle fibers and that during muscle relaxation there is a cosilence (Vallbo, Hagbarth, Torebjörk and Wallin 1979; Burke, Hagbarth and Wallin 1980). This means that as long as the receptor bearing muscle remains relaxed, spindle endings are probably not exposed to any fusimotor drive and also, that a selective fusimotor activation cannot account for a change in reflex amplitudes.

Some studies question the necessity of a strict coupling between the alpha and gamma motor system (e.g. Vallbo and Hulliger 1981). Recently, it was even shown that during the relaxed state in the awake cat there was not always a cosilence; direct recordings from efferent fibers revealed that selective activation of fusimotor fibers occurred spontaneously or could be induced (Ribot, Roll and Vedel 1986). Whether this mechanism actually explains reflex changes during a foreperiod in man, however, is still open to question. Experimental work by Gerilovsky, Struppler, Altmann and Velho (1983) suggests that during the foreperiod and in relaxed muscles, reflex modification takes place independent of the fusimotor system.

An alternative way for the CNS to modulate reflex responses is by affecting the transmission at the Ia afferent-alpha motoneuronal synaps in the spinal cord, or by regulating the amount of transmitter release at the Ia afferent terminal through fibers that make contact presynaptically.

It is also possible that interneurons are involved in the T-reflex, and thus that this reflex might not be exclusively monosynaptic (Burke, Gandevia and McKeon 1984). It appears that influences from intramuscular as well as extramuscular sources converge on these interneurons (Lundberg 1979; Jankowska and McCrea 1983). Although the fast conducting Ia fibers contribute mainly to the afferent path of the reflex, as was shown by Lloyd (1943b), sensory systems from the skin and joints might play a role as well, because of the interneurons used in common by the Ia and other afferent fibers. In fact, it has been shown that H- and T-reflexes are facilitated by cutaneous stimulation of even remote sensory nerves (Delwaide and Crenna 1984). Also, Achilles tendon percussion was shown to activate not only mechanoreceptors in the muscle that is stretched, but mechanoreceptors in other muscles, for instance small muscles in the foot, and mechanoreceptors in the skin as well (Burke, Gandevia and McKeon 1983). Based on their distance from the cord and the conduction

velocity of their axons, it might be concluded that these sense organs all affect reflex discharge. This is not surprising if one takes into account that the effective stimulus for the tendon jerk might not be muscle stretch per se, but rather the resulting vibration wave that spreads through the muscles and bone of the lower limb (Lance and De Gail 1965). The functional significance of this complex afferent innervation, however, is related to movement. The existence of some neuronal connectivity per se does not imply its involvedness in all parts of our behavior. It is conceivable, for instance, that activity in group Ib, group II or group III muscle afferents or in afferents from skin and joints does contribute to reflex discharge. But since we are interested in phasic and instruction dependent reflex changes that occur in the absence of overt movement, the role of these (indirect) circuits is probably of minor importance.

Our attention in the next section, therefore, will be directed mainly on the higher neural centres that modulate information transmission in the reflex arc, either at the monosynaptic connection of afferent fiber and motoneuron, at the interneuronal level, or presynaptically.

3. Possibles sources of supraspinal activity affecting reflex discharge

The four main descending systems in man, corticospinal, vestibulospinal, reticulospinal and rubrospinal, appear to have connections with motoneurons that are either exclusively or predominantly polysysnaptic (Baldissera, Hultborn and Illert 1981). The descending fibers project to a much larger extent on segmental interneurons than on motoneurons themselves. By this arrangement, reflex amplitudes are influenced by activity from peripheral and central structures in an integrated fashion.

Besides these postsynaptic influences, both facilitatory and inhibitory, there exists a presynaptic inhibitory mechanism that can modulate reflex amplitudes by depolarization of primary afferent terminals (PAD). Depolarization is thought to be brought about by axo-axonal synapses and to hamper information transmission by an inhibition of transmitter release (Eccles 1964). Presynaptic inhibition seems to be widespread in the spinal cord. It is considered as much a controlling factor in reflex excitability as are changes in the excitability of the motoneurons themselves (Delwaide 1973).

Presynaptic inhibitory influences may originate from a variety of sources, both segmental and supraspinal. With regard

to influences from the brain it was found for instance, that stimulation of the sensorimotor cortex could produce PAD (Andersen, Eccles and Sears 1964). Some sort of somatotopical organization was found to exist by the latter authors, in that somatosensory arm and leg areas acted predominantly on the arm and leg afferent fibers. Probably, such actions were accomplished by corticospinal fibers innervating complex interneuronal networks (Carpenter, Lundberg and Norrsell 1963).

That presynaptic inhibition might actually play a role in the reflex changes observed during various degrees of alertness is suggested by the finding that this mechanism is probably involved in the reflex decrease that has been observed during desynchronized sleep (Baldissera, Cesa-Bianchi and Mancia 1966; Pompeiano 1967). Findings such as these, however, derive largely from experiments in the cat. Some precaution is needed when they are applied to man. Another important finding is that Ia and Ib afferents are not necessarily affected by the same PAD pathways; PAD from sensorimotor cortex, for instance, appears to affect Ib muscle afferents exclusively (Andersen, Eccles and Sears 1964; Jankowska 1984). These complicating features prevent a clear understanding of the significance of presynaptic inhibition with regard to reflex control in man.

A schematic representation of the components of the reflex arc and of the supraspinal influences acting upon it is given in Fig.3.

Which cerebral structures could be responsible for the post- and presynaptic effects on reflex excitability during motor preparation?

The prime structure in the central control of movement is the precentral (motor) cortex. Its significance has been undisputed since the discovery by Fritsch and Hitzig (1870), that electrical stimulation of this part of the neocortex elicits movement in the contralateral musculature. Now it appears that the same structure (area 4 according to Brodmann's classification) shows changes of neuronal activity during the preparation to act and in the absence of overt movement or changes in EMG output. Some of the cells in this brain area showed increased activity during a waiting period of several seconds, prior to a learned movement that was to be executed by a monkey upon the occurrence of an external event (Tanji and Evarts 1976). However, contemporary views on motor organization seem to stress the fact that the role of the motor cortex in movement initiation and execution is comparable to the role of the motoneuron at the spinal level, i.e. that it is a final common pathway only and that activity in other brain centers generally

precedes motor cortex activity (Evarts 1979; Kornhuber 1984).

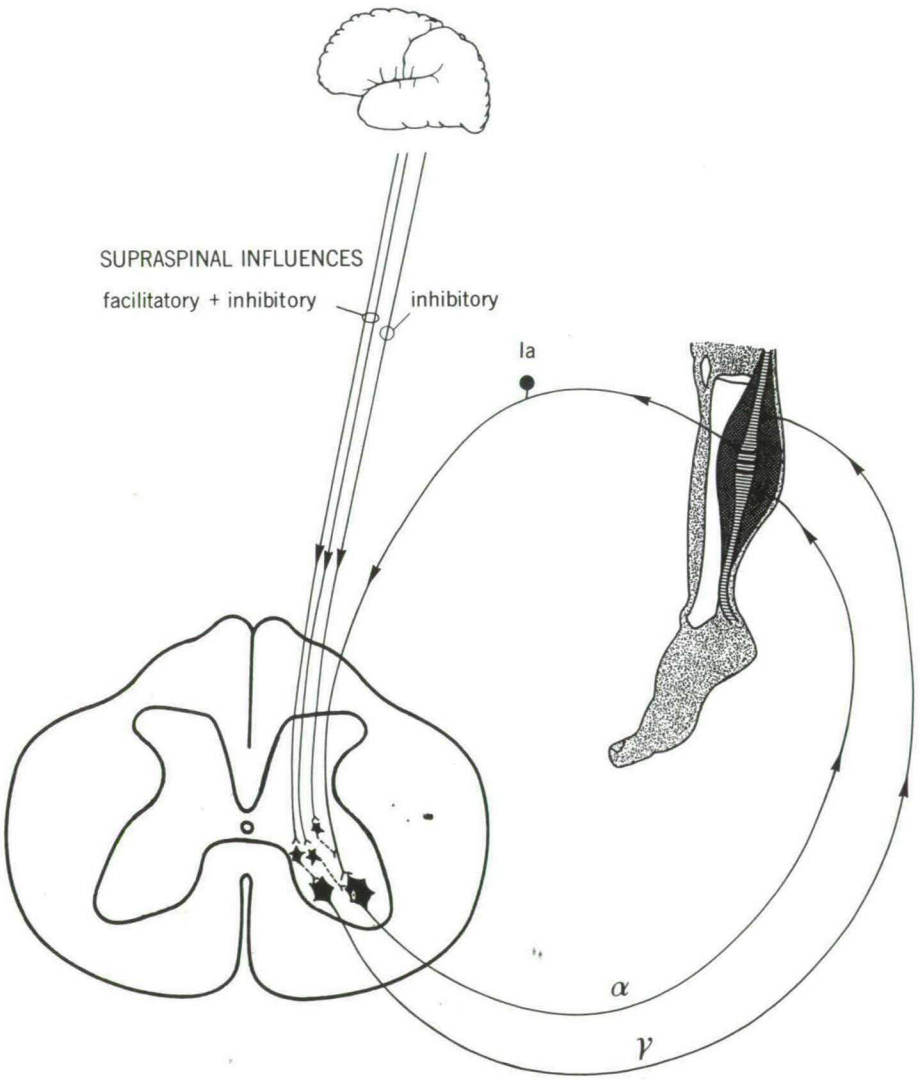

Fig. 3 Components of the reflex arc.
The extended central structure in the muscle at the right is the muscle spindle. When the muscle is stretched, the spindle's primary endings are activated and an afferent volley is caused to travel, via group Ia fibers, to the spinal cord. In the cord, there is a chiefly monosynaptic connection with the alpha motoneurons which innervate the muscle.
Supraspinal influences have an effect on reflex discharge by acting predominantly on spinal interneurons (dotted lines). Postsynaptic effects are either facilitatory or inhibitory. Presynaptic effects are inhibitory only.

A cortical area that might be of importance in this respect is the supplementary motor area (SMA), which is part of Brodmann's area 6 and is located along the mesial walls of the cerebral hemispheres (see Fig.4 for a classification of cortical areas according to Brodmann). Activity in this part of cortex was found to be increased during a motor preparatory period, just as was activity in motor cortex (Tanji, Taniguchi and Saga 1980). When monkeys performed extension or flexion movements of the wrist that were triggered by a visual or auditory signal, response latencies of SMA neurons were found to be about 30 msec shorter than latencies of neurons in precentral cortex (Tanji and Kurata 1982). Also, regional cerebral blood flow studies indicate that SMA is the only cortical region active when subjects imagine the performance of a motor sequence without executing it (Roland, Larsen, Lassen and Skinhøj 1980). Finally, a complex of three slow potentials can be recorded from the human scalp from about one second prior to self paced voluntary movements, which are called Bereitschaftspotential (BP), premotion positivity (PMP) and motor potential (MP) respectively. Studies on the topographical distribution of these slow waves have revealed the important role of SMA in the generation of both BP and PMP (Deecke and Kornhuber 1978; Deecke, Heise, Kornhuber, Lang and Lang 1984). Observations such as these suggest that SMA is especially involved in the process of motor programming or establishing a preparatory state, rather than in the actual execution of a movement. The efferent connections that were shown to exist in the monkey, from SMA to the spinal cord (Macpherson, Wiesendanger, Marangoz and Miles 1982) and from SMA to the motor cortex (Jones, Coulter and Hendry 1978), could provide the neuronal basis for changes in both reflex excitability during preparation and the effectiveness of the subsequent motor response. SMA activity, however, was found to depend on the type of motor task employed. Simple finger flexions, in contrast to more complex movement sequences, did not involve SMA activity in the Roland, Larsen, Lassen and Skinhøj (1980) study.

Anticipatory functions with regard to motor performance have also been ascribed to the premotor cortex (lateral part of area 6) (Weinrich, Wise and Mauritz 1984), parietal cortex (area 5 and 7) (Mountcastle, Georgopoulos, Sakata and Acuna 1975) and prefrontal cortex (area 8, 9 and 10) (Fuster 1981). Evidence as to the exact motor functions of these cortical regions is inconclusive, however. The role of the somatosensory cortex (area 1, 2 and 3), on the other hand, seems to be an unsignificant one (Lamarre, Spidalieri and Chapman 1983). The significance of this part of the cortex is probably limited to so called closed loop

movements, a type of movement that relies on kinesthetic information during execution (Evarts 1979).

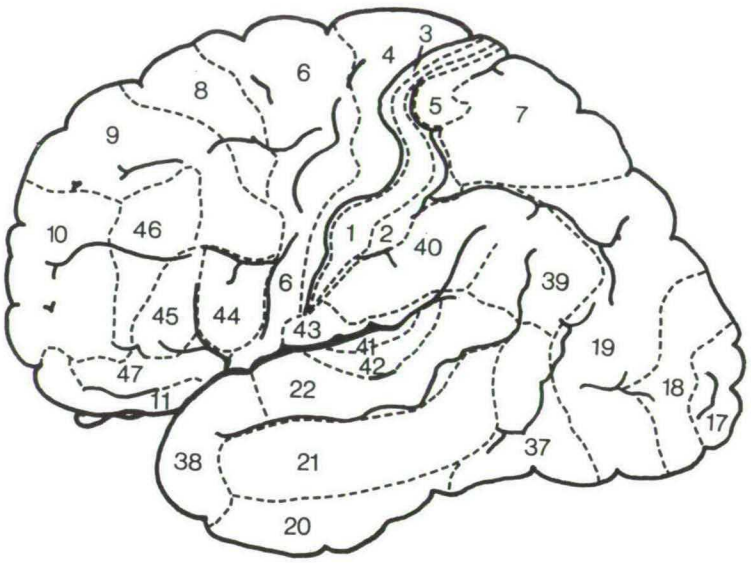

Fig. 4 Cyto-architectonic areas in the left cerebral hemisphere, according to Brodmann.

In addition to the cortical areas, some subcortical structures have to be considered for their possible role in the preparatory motor process. These are the basal ganglia and cerebellum, which were found to become active prior to the motor cortex in the execution phase of a movement (Thach 1975; Soltysik, Hull, Buchwald and Fekete 1975), while blocking of these structures resulted in impairment of goal directed movements (Beaubaton, Trouche and Amato 1980). The efferent fibers of the cerebellum appear to terminate in the premotor and motor cortical areas, whereas the basal ganglia probably project, via the thalamus as a relay system, to SMA only (Massion and Rispal-Padel 1986; Strick 1986). Thus, the two subcortical systems provide pathways to the cortex that are, at the subcortical level, completely separated. It seems reasonable to assume, therefore, that the cerebellum and basal ganglia are also distinct with regard to their function. One of the speculations

that can be made is that the basal ganglia, because of their exclusive connections with SMA, are of special importance in the motor preparatory process. Evidence that is consistent with such a view is now being collected. Rolls, Thorpe and Maddison (1983), for instance, showed in the monkey that many neurons in specific parts of the basal ganglia, i.e. in the head of the nucleus caudatus and the anterior part of the putamen, increased their firing rate in response to stimuli that served as cues for future movements, but not in response to stimulus presentation or movement per se.

In recent motor theories, the planning of a voluntary movement (Kornhuber 1984) or the development of a motor program (Brooks 1979) is thought to take place in the abovementioned subcortical regions or in the frontal, temporal and parietal association cortices. From cerebellum and basal ganglia information is assumed to be relayed, via the thalamus, to the cortex (SMA, premotor and motor cortex) again and from there down to the spinal cord.

Although the evidence about what supraspinal structures affect reflex discharge remains inconclusive, there are strong indications against an exclusive or even privileged role of the motor cortex. Instead, the data favor a distributed system theory of movement (Kornhuber 1984). The theory states that several neuronal systems, cortical and subcortical, are involved in the planning, initiation and execution of voluntary movements. An implication of such a theory might be, that the control of movement is not necessarily hierarchically organized. In such a view, holistic qualities on the one hand and detailed aspects of a movement on the other might be represented in parallel by activity in different brain systems. We assume, as a working hypothesis, that reflex changes observed during a foreperiod provide us with information about the overall activity level in these movement related brain structures.

Chapter III.

Preparation for a movement

III. PREPARATION FOR A MOVEMENT

1. Theorethical considerations

When a subject is provided with a warning signal (WS) indicating the arrival of a second signal (RS) that requires a motor response, the reaction time (RT) is generally shorter than when an imperative signal is presented alone. The optimal duration of the foreperiod seems to be about 0.5 second or even less (Näätänen and Merisalo 1977).

Obviously, performance is facilitated by processes intervening between WS and RS. These processes have been given various names, such as attention, set, tuning, programming, expectancy or motor preparation, to name just a few. Despite the different connotations attached to these concepts, the efficiency of the underlying processes seems to be related to a common notion: the subject's imperfect ability to estimate the length of the foreperiod, or his time uncertainty (Klemmer 1957). In case of a simple RT task with foreperiod duration held constant over blocks and other things being equal, the difficulty in predicting the exact moment of stimulus presentation is the sole variable determining the subject's performance (Näätänen 1972). In studying spinal reactivity changes prior to movement, we have made ample use of this type of experimental paradigm, as will be described in the next chapter.

We prefer to use the term preparation or motor preparation to designate the intervening processes described above, as such a concept clearly refers to the subject's performance level and thus allows for operationalization better than do some other concepts (Requin 1980). It should be noted, however, that although the term refers to motor output, it is meant to include all other processes that improve reaction time performance.

The processes that improve performance are, according to Niemi and Näätänen (1981), both perceptual and motor. Perceptual processes are attending to the stimulus and, probably, rehearsing the mental image of the stimulus. They would facilitate detection of the stimulus when it is delivered. The motor processes are believed to include an increase of the response system's activity level toward the action limit. When this limit is reached, either at the moment the RS is presented or prematurely, a motor response ensues. In this view, the preparatory state and the actual response are not qualitatively different; preparation flows into execution by adding to the pre-existent level of activation, without a threshold being passed (see also Meyer

1953).

Niemi and Näätänen (1981) point to several factors that affect these perceptual and motor processes and that determine the general level of preparedness. Some of these factors are related to expectancy. Expectancy is defined as the subjective probability that the RS will be presented immediately. In the simple RT paradigm, this concept is closely related to time uncertainty which, in turn, is affected by foreperiod duration. During fixed foreperiods of some seconds, expectancy is thought to increase toward the end, the time course having a long flattened-out form in the beginning but peak expectancy being reached at the moment the RS is presented (Näätänen and Merisalo 1977).

Other factors are unrelated to expectancy and affect the level of preparedness directly. The first is short-term exhaustion and fatigue, indicating that peak readiness cannot be maintained for long; this factor might counteract an expectancy level that has otherwise been increased, i.e. it explains why after longer foreperiods RTs are generally lengthened. The second factor is immediate arousal; an intense auditory stimulus used as RS, in contrast to a visual or less intense stimulus, has a facilitating effect upon performance (Sanders and Wertheim 1973). This effect is capable of counteracting the slowing down of RT due to increased time uncertainty. The third factor is a change in stimulus criterion. Niemi and Näätänen (1981) suggest that the criterion for RS detection is influenced by WS intensity. It appears, however, that WS intensity effects on RT are rather ambiguous (Niemi 1982). The next factor is speed-accuracy trade-off. This factor is proposed to influence the subject's response criterion. The instruction given to the subject to be either fast (and to allow for more premature responses as a consequence), or to be accurate (and to respond slower) seems to be the crucial variable here. Speed instructions increase the level of preparedness, while accuracy instructions exert an inhibitory effect. The fifth and last factor is called fluctuations in preparedness due to inaccuracies in control. These are changes in the level of preparedness that are centrally initiated but rely on feedback from the muscles. They are meant to correct for fluctuations away from the action limit that occur more or less spontaneously.

In the experiments presented in this thesis, neuronal changes recorded at the spinal level might perhaps be related to some of the above factors. As foreperiod duration (affecting expectancy and short-term exhaustion) as well as stimulus parameters (affecting immediate arousal and stimulus criterion)

were held constant across the experiments, speed-accuracy trade-off and fluctuations in motor preparedness are the most relevant factors with regard to our work. Some of the divergent results that we found in different experiments, for instance, might be accounted for by differences in instructions given to the subjects with regard to speed or accuracy. The second factor, fluctuations in motor preparedness meant to correct for unwanted excursions away from the action limit, might have been reflected in the reflex changes that we observed from one trial to another. However, since we were interested in the general characteristics of preparatory adjustments in the spinal cord, we choose to average the data from individual trials. Therefore, we cannot speculate on the nature of these corrective fluctuations, unless they would appear time-locked to the stimuli and not occur on a random basis.

An interesting question is whether steps identified in the reaction process by experimental psychologists on the basis of (choice) RT research (Sanders 1980a), can be compared to the physiological findings obtained at the surface of the human body, as in our work, or by recordings of activity in movement related brain structures, that are usually made in the monkey.

Requin, Lecas and Bonnet (1984) regard this as a fruitful attempt. These authors propose a three step model of motorpreparation, in which the first functional stage in motor organization, namely the definition of an action goal or the retrieval from memory of the appropriate response, might be structurally represented in the cortical association areas. The second step then would be the building of a motor program, that is, specification of the biomechanical parameters of the movement in advance of its execution. The brain structures related to this function might be the cerebellum and the basal ganglia. The ultimate step is movement execution, this function being represented primarily in the motor cortex.

Although there is ample evidence, reported earlier, that some brain structures are activated well in advance of the motor cortex, and also that activity in some of these structures is probably affected by manipulations of variables that influence performance, such as response probability (Requin, Lecas and Bonnet 1984), there remains a major concern. That is whether the stages identified in the RT literature, usually proposed to be activated after the go-signal, are also the processes that take place during the foreperiod, when the aim is rather to withhold than to let go.

At present, we prefer to view the processes during the foreperiod as not necessarily comparable to the ones described by

Sanders (1980a). The main argument is that the latter processes take only a few hundred milliseconds to be completed. During foreperiods of some seconds and with simple stereotyped movements, such as the finger and foot flexions employed by us, response selection from memory and motor program building would not, in all likelihood, be very time consuming. This is not to say that part of the response, and part of the processes generally thought to take place after the response signal, cannot be executed in advance, i.e., during the foreperiod. What is done during the foreperiod of a simple RT task then, is in our opinion best decribed by a global reference to perceptual and motor processes that facilitate performance, as was done by Niemi and Näätänen (1982).

Now let us take a closer look at the nature of these processes. When the subject is informed about an imperative visual stimulus to be presented, he will shift his gaze and focus the spot of future stimulation. Such a peripheral attentional mechanism is necessary for detection, as it brings the stimulus in the subject's visual field. Focusing might also be beneficial by increasing visual acuity, because of the greater density of cones in the central part of the retina. This seems especially relevant in tasks requiring the detection and identification of details, which is not the case here. However, attentional mechanisms need not be limited to receptor adjustments.

Posner (1980) showed that reaction times to peripheral stimuli are faster when subjects are told to attend to the location of the stimulus while fixating elsewhere, than when they were told to attend elsewhere. In such a situation it is not easy to see that attention is a purely perceptual process, because motor responses are also involved. In an attempt to differentiate between the sensory and motor effects of set on perception, Haber (1966) concluded that there was strong evidence favoring the role of response processes, although the possibility of perceptual enhancement could not be ruled out. Sanders (1980a) even argued that foreperiod duration, which influences attention, does not affect any of the early perceptual stages in the reaction process, but rather the last stage intervening between imperative stimulus and response which is called the motor adjustment phase. He proposed that "quite possibly, preparatory activity for detecting a signal consists largely of motor adjustments" (Sanders 1980a). Such a conclusion is hard to reconcile with the results of a regional cerebral blood flow study by Roland (1981), who demonstrated an increased activity in the somatosensory finger and mouth area of the human cortex, when subjects were asked to focus their attention upon the tip of their index finger

or the upper lip, respectively. The subjects were told that they could expect tactile stimuli which were just above threshold at either of these body locations. They were instructed to count the stimuli during a period of time and report the number afterwards. No muscular contractions were observed during the test period. Blood flow increases were observed even prior to actual presentation of stimuli. Since the somatosensory area seems to play a minor role in open loop movements, as argued earlier, and since the regional cerebral blood flow changes were limited to the areas corresponding to the body parts to be stimulated, we would like to take this as evidence that attentional mechanisms may also imply tuning of relevant sensory systems and do not only rely on motor adjustments.

What about the motor processes then, that occur prior to movement? It has been found that subjects, when instructed to wait for and respond to a particular stimulus, sometimes tense muscles which are relevant to the response in advance, and that they do so even without explicit instruction (Brunia and Vingerhoets 1980; Burke, McKeon, Skuse and Westerman 1980; Haagh and Brunia 1984). The amount of tension during a foreperiod was found some decades ago to be inversely related to response speed (Davis 1940, referenced to in Courts 1942). Also, induced muscular tension has been found to facilitate RT performance (Freeman and Kendall 1942; Sanders 1980b). This is clear evidence that increasing the activity level toward the motor acton limit is indeed effective as a preparatory mechanism.

In summary, we propose that the attentional and motor preparatory processes during a fixed foreperiod consist of 1. receptor and/or bodily adjustments, 2. tuning of relevant sensory systems and 3. increasing the motor system's activity level. The reflex technique might be helpful in revealing some of the changes related to these processes that remain unaccessible to surface EMG recordings.

2. Psychophysiological changes accompanying preparation for a movement

Apart from the tensing of response-relevant muscles that is sometimes apparent from surface EMG recordings, and apart from more subtle changes in spinal reactivity that can be revealed by employing monosynaptic reflexes and that will be described hereafter, there are other physiological parameters showing systematic changes during the foreperiod of a reaction time task. These changes illustrate that preparation for a movement is not

only a matter of increasing the response system's activity level, but that it involves widespread adjustments in both the somatic and the autonomic nervous system, the functional significance of which, however, is often not known. Also, whether such changes appear exclusively prior to movement is a subject of discussion.

First, EEG recordings have revealed the existence of a cortical slow negative wave called contingent negative variation (CNV). Initially, this wave was related to expectancy (Walter, Cooper, Aldridge, McCallum and Winter 1964). Later, when foreperiod duration was extended from 1 to 4 seconds, an interval that permits comparison with slowly developing visceral changes, the CNV was shown to be built up of two distinct components. The CNV early wave peaked between about 0.5 and 1 second after the beginning of the foreperiod and was considered an afterwave associated with the WS, while the late wave began about 1.5 second before the RS and was associated with response execution (Rohrbaugh, Syndulko and Lindsley 1976). Probably, the CNV pattern does not depend on the two-stimulus paradigm for its occurrence, but is for a large part determined by 1. an orienting response to the WS and 2. a Bereitschaftspotential that occurs also prior to a non-triggered voluntary movement (Rohrbaugh and Gaillard 1983). So, on the cortical level, the increase in negativity seen during the second half of the foreperiod seems to be related to motor preparation.

Another variable is the evoked cardiac response. The heart rate pattern commonly observed during a foreperiod consists of three phases that are hold to reflect different psychological processes. The first phase is a deceleration that is time-locked to the warning signal. The view that is generally accepted with regard to this deceleration is that it is, again, an index of the orienting response (Graham and Clifton 1966). However, arguments contradictory to such a view and favoring an interpretation of the deceleration as a sign of stimulus processing have also been presented (see Barry 1986).

The second phase is an acceleration which, in the two-stimulus paradigm, was proposed to be related to anticipation of significant aspects of the stimulus (Lang, Öhman and Simons 1978). In contrast to this explanation, acceleration was very prominent in a control task where the second stimulus lacked significance (Somsen, Van der Molen and Orlebeke 1983).

The third phase, a deceleration occurring during the second half of the foreperiod, was held to depend on response performance (Lang, Öhman and Simons 1978), but recently was found to be present during the anticipation of noxious stimuli as well (Somsen, Van der Molen and Orlebeke 1983). Both sensory and motor

processes seem to be related to this phase (Coles 1984).

It can be concluded that, whereas the first phase is stimulus related, the functional significance of the second and third phase remains to be established (Bohlin and Kjellberg 1979), and that their relationship to movement is not completely clear.

Two other parameters that have been investigated during and prior to RT performance are the cutaneous eye-blink reflex and pupillary diameter.

The blink reflex is known to consist of two components, the first having a latency of about 10 msec and being probably oligosynaptic, and the second having a latency of about 40 msec and being polysynaptic. Both components involve connections between the trigeminal and facial cranial nerves, the second component probably also traversing some nuclei in the brain stem reticular formation (Hiraoka and Shimamura 1977; Ongerboer de Visser and Kuypers 1978). Consideration of the behavior of the blink reflex during RT tasks seems relevant, as muscles are involved in this reflex that bear no clear relationship to movement. The cutaneous eye-blink is generally considered to have a protective function. This is contrary to reflexes evoked in the extremities, where the effector muscles are often directly involved in the impending movement, or might play a role in postural adjustments accompanying movement. From a comparison of blink and limb reflexes then, insight can be gained about whether during motor preparation the response system is primed selectively, or whether motor preparation is characterized by a diffuse change in outflow reflected in potentially relevant and irrelevant reflex circuits alike.

It was shown that during preparation for a movement, whether a limb movement or an eye-lid response, the amplitudes of the first and second components are affected differentially. The first component is generally potentiated while the second is depressed (Boelhouwer 1982; Sanes 1984). The function of the second component is considered to be displacement of the eyelid (Shahani and Young 1973), while the function of the first is still not known. The first component is, however, considered to reflect gross behavioral state (Sanes 1984) or arousal (Boelhouwer and Brunia 1977). For that reason, the behavior of the first component seems to be of prime interest. The modification of this component was shown to follow a time course roughly comparable to the CNV pattern described above; first there was a short latency excitability increase following the WS. Then, after a decline, there was a heightened excitability persisting until the end of the foreperiod (Boelhouwer 1982) or

gradually increasing towards RS presentation (Sanes 1984).

Besides heart rate, a second autonomic variable that has been studied during warned RT tasks in recent years is pupillary diameter. Pupillary diameter has been considered to reflect variations in processing load during a variety of cognitive tasks (Beatty 1982). It was shown that during the 3 sec foreperiod of a warned RT task pupillary dilations occurred, the time course of which again resembled the CNV waveform (Richer, Silverman and Beatty 1983). The slowly increasing dilation towards the end of the foreperiod was thought to primarily reflect response preparation, based on the similarity between this increase in diameter and the slow dilation found to develop prior to self-triggered movements (Richer and Beatty 1985).

The above evidence suggests that the effects of the induced intention to move are widespread and that they can be recorded as changes in activity of both the somatic and the autonomic nervous system. Also, although nothing is known about their functional interdependence, changes in EEG, blink reflex and pupillary diameter show striking similarities: a first activity increase is seen immediately after the WS and a second one developing slowly towards the end of the foreperiod. The heart rate pattern is the only exception. It is not di- but triphasic. In all variables, however, activity changes at the beginning of the foreperiod appeared to be related to stimulus processing in some sense, whereas motor preparation seemed to be manifested primarily during the final half of the foreperiod.

Chapter IV.

The present experiments

IV. THE PRESENT EXPERIMENTS

1. General methodology

The experiments were performed on subjects sitting in a sound-proof and electrically shielded cubicle. The subjects were seated in a specially devised chair, with their knees and ankles being flexed at about 120 and 90 degrees, respectively. Special devices attached to the chair kept the legs in the specified position. Keeping the legs fixed is important, as even minor changes in the angle of the ankle joint are able to influence motoneuron excitability: passive dorsiflexion generally results in a relative depression, while passive plantar flexion results in an increase of reflex amplitude (Paillard 1955; Robinson, McComas and Belanger 1982). The subjects' feet were placed on moveable footplates with microswitches underneath for the recording of (foot) RTs. Microswitches were also mounted in the chair arms for the recording of manual RTs.

Reflexes were evoked by vibration exciters, directed at a right angle to the Achilles tendons. The vibration exciters were triggered by rectangular electrical pulses of 9 msec duration. After the intensity of the tendon taps had been adjusted in such a way that steady reflex responses of about equal amplitude could be obtained from both legs, the reflex eliciting stimuli remained unchanged. This was done to ensure constant intensity of the tap and a nonchanging site of tendon stimulation throughout the experiments, as was recommended by Hugon et al. (1973). To obtain a global indication of the electrical activity of the muscles, pairs of Ag-AgCl surface electrodes were fixed on the distal parts of the left and right soleus muscles and in some cases on the bellies of the anterior tibial muscles, with an interelectrode distance of about 5 cm.

Inside the cubicle, there were devices for presenting auditory and visual stimuli, as well as a set of preamplifiers for amplification of the EMG signals. The apparatus placed outside the cubicle, in the experimenter's room, consisted of endamplifiers, a control panel for starting and stopping the experiments and for visual inspection of the EMG signals, and a PDP Lab 8e computer by which the experiments were controlled. All EMG signals and the necessary trigger signals were recorded on magnetic tape. RTs were collected on paper tape. The EMG signals were subsequently fed into a PDP 11/10 computer for analysis (analog to digital conversion and determination of the peak to peak amplitudes of the reflex potentials, and integration of the

background EMG). Final calculations were done on a VAX 11/782 computer.

Fig.5 gives a schematic overview of the above, indicating the position of the subject, the locations of the recording electrodes and reflex eliciting devices, and the apparatus used for stimulus presentation and storage and analysis of the data.

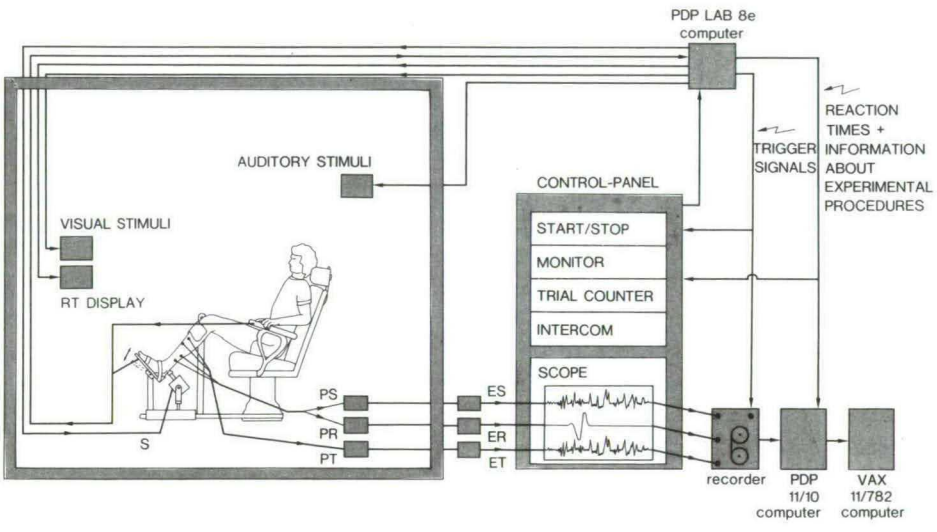

Fig. 5 Schematic representation of the experimental arrangements.
PS, PR and PT refer to preamplifiers and ES, ER and ET refer to endamplifiers for Soleus EMG, T reflexes and Tibialis anterior EMG, respectively.
RT refers ro reaction time.
S refers to the reflex eliciting stimulus.
For further explanation: see text.

2. Experiment I: The time course of motor preparation

In the first experiment (see Appendix 1 for an extensive description), the general time course of preparation was studied. Reflexes were evoked at several latencies during a fixed foreperiod of 4 seconds and shortly after the foreperiod, prior to and during movement execution. As the response served a plantar flexion of the right or left foot, or a right or left finger flexion, each type of response occurring blocked.

In case of a unilateral foot response the responding member is called involved in the response and the contralateral member is uninvolved. In case of a manual response both lower limbs are called uninvolved in the response. As a T-reflex and a voluntary plantar flexion are brought about by the same muscles, the T-reflex technique thus allows for a differentiation of activity in both response involved and noninvolved neuronal systems, or for a distinction between generalized (diffuse) and selective aspects of the motor preparatory process. As we will see, selectivity appeared to be a major hallmark of the motor preparatory process studied at the spinal level.

The results showed a short latency rise in reflex excitability, due to presentation of the warning signal. This early peak is the subject of further investigation in Experiment II. After this peak reflex amplitudes were found to subside slowly and again to rise slightly towards the end of the foreperiod. The general activation pattern was comparable to the slow cortical potential, blink reflex and pupillary diameter data that were discussed in chapter III.2.

It was suggested (Brunia, Haagh and Scheirs 1985) that the early peak and the sustained excitability increase immediately thereafter reflect the processes of orienting to and evaluation of the warning signal, while motor preparatory processes, again, are likely to be reflected in the second reflex increase, from about 2 seconds onwards during the foreperiod.

The results described sofar concern reflex changes in the noninvolved leg. From the beginning of the foreperiod the excitability changes in the involved leg behaved differently in that they stayed closer to the baseline and did not even differ significantly from it during the later part of the foreperiod. This differential reflex effect was interpreted as being due to a presynaptic inhibitory mechanism (see Appendix 1). Its function was supposed to be protection of the agonist motoneuronpool against external disturbances which could interfere with the reaction process. However, more recent evidence indicates that such an interpretation can be challenged (see Experiments III and

IV). Rather than by a selective neuronal inhibition, it now appears that the differential effect might be accounted for by a change in peripheral stimulation parameters.

Whatever the mechanism, the differential effect has been a consistent finding both in experiments from our laboratory and in experiments described by a French group of researchers (e.g. Requin 1969; Requin and Paillard 1971). However, there are also some discrepancies between the evidence collected by the latter group and our data, as was pointed out by Brunia (1983). The discrepancies concern the general time course of the reflexes in the involved leg (i.e. is there an increase or a decrease during preparation?); they also concern the question whether T- and H-reflexes show similar or distinct excitability curves.

A major cause of the discrepancies might lie in the fact that z-score transformations were used by the French investigators. Their z-scores were calculated according to an improper algorithm, in which the standard deviation (SD) and mean of the control reflexes were used, instead of the SD and mean of the complete sample of experimental and control reflexes (see Bonnet, Requin and Semjen 1981; Requin, Lecas and Bonnet 1984). When the mean and SD are taken from a distribution different from the X-distribution, the main characteristics of z-scores (mean = 0; SD = 1) are lost. When z-scores have been calculated in this way, the amount of reflex change depends primarily on the variability of the control reflexes. A high peak in one condition as compared with another, for instance, might simply indicate a lower variability of the control reflex. Furthermore, as it is plausible that control reflexes vary less than do the experimental reflexes, a consequence might be that the size of reflex changes during foreperiod is generally overestimated as compared with a procedure employing properly calculated z-scores or transformations into percentages. This taking of the control reflex variability as the unit of measurement makes it impossible to assess whether the difference between curves is real and thus to conclude that there does or does not exist a differential effect. Finally, z-score transformations per se do not make a skewed distribution symmetrical, which was in fact suggested by Bonnet, Requin and Semjen (1981) and by Requin, Lecas and Bonnet (1984) and presented as an argument in favor of a transformation into z-scores instead of percentages. We are thus forced to the conclusion that inferences from these reports regarding both the amplitude of reflex modulations observed during foreperiod and the differential effect might seriously be in error.

Some differences, however, remain and cannot be explained by the use of z-scores. These concern the general time course and

the question whether T- and H-reflexes behave similarly. Although the similarity versus dissimilarity of T- and H-reflexes was not a subject of the present investigations, growing evidence indicates that the dissimilarities are larger than ever before assumed (see Burke 1983; Van Boxtel 1986). So, the modifying factors for both types of reflexes are not necessarily the same and, unless these factors can be specified exactly, a comparison of T- and H-reflexes across different studies seems less valuable to us.

When French studies (Requin 1969; Requin and Paillard 1971) are compared to ours with regard to the T-reflex time course only, it is the absolute reflex decrease in the former as opposed to a decrease that's only relative to the first peak in the latter, that is most apparent. The only explanation that we can provide for this is the one presented in Experiment IV, saying that when there is more background muscle tension there is also more reflex depression. In the Requin (1969) and Requin and Paillard (1971) experiments, 1 second foreperiods were used. It is not unlikely that muscle tension was, in fact, larger in these short foreperiods than in the longer ones employed by us.

After the response signal in the present experiment, reflex amplitudes rose two- to sixfold both when the soleus muscle was involved and noninvolved. This effect was more prominent in the involved muscle and the peak amplitude was also reached earlier. Such an increase in the amplitude of monosynaptic spinal reflexes occurring shortly before voluntary movement has been well documented, both when the receptor bearing muscle functions as agonist (e.g. Pierrot-Deseilligny, Lacert and Cathala 1971; Michie, Clarke, Sinden and Glue 1976; Kots 1977) or does not take part in the movement (e.g. Bowditch and Warren 1890; Paillard 1955; Coquery and Coulmance 1971). In these studies, a time lag was generally reported between the rise of monosynaptic reflexes and the rise in surface EMG activity accompanying movement. Haagh, Spoeltman, Scheirs and Brunia (1983), however, argued that EMG onset is a concept that is often ill defined, and that no signs of a time difference are evident when an alternative method of relating reflexes and EMG activity is employed. In line with this argument, we propose a supraspinal drive enhancing alpha motoneuron excitability as an explanation for the large reflex increase prior to and during the actual movement. This is in contrast with an explanation in terms of a decreased presynaptic inhibition that has also been proposed (Pierrot-Deseilligny, Lacert and Cathala 1971). There is indirect evidence that monosynaptic excitatory connections from cortex to soleus are small or absent in man (Cowan, Day, Marsden and

Rothwell 1986). Thus, probably, the excitability increase is effectuated via interneuronal networks.

The mechanism underlying the sharp reflex decrease in the involved muscle at only 300 milliseconds after the response signal is even less clear. In Appendix 1 it is argued that the poorer contact between hammer and tendon could be held responsible for this effect. The sole contribution of this peripheral factor must at present be questioned, however.

Recent evidence indicates that sudden release of the calf muscles from a tonic isometric or isotonic contraction results in a sharp decrease of T-reflexes, which is primarily due to a descending inhibitory influence acting presynaptically on the Ia afferent fibers. Such an active inhibition appears to be characteristic for muscle release (Schieppati and Crenna 1984, 1985). That it is the neural command accompanying muscle release that causes this sharp decline is further suggested by the observation that the H-reflex shows a time course similar to the tendon jerk during muscle tension and relaxation (Coquery and Coulmance 1971; Schieppati and Crenna 1984) and that the H-reflex is not inhibited when the foot is not returned but maintained in the plantarflexed position (Gottlieb and Agarwal 1978).

In Chapter III of this thesis, we followed Requin (1980) in proposing a definition of motor preparation in terms of performance. If T-reflex amplitudes reflect motor preparation, one would expect a relationship to exist between reflex amplitude and performance. We intended to calculate coefficients of correlation to solve this question. But since few reflex values had been obtained at a given point in time for each subject, calculations were restricted to an intersubject analysis. Both reflexes at the end of the foreperiod (at 3900 milliseconds after WS onset) and just afterwards, during movement initiation (at 4100 milliseconds) were considered. The results are given in Table I.

Table I. Interindividual coefficients of correlation between reflex amplitudes and reaction times

response mode	recording side	points in time 3900	4100
right foot	right soleus	.18	-.27
	left soleus	.19	-.09
left foot	right soleus	.02	.17
	left soleus	.19	-.04
right hand	right soleus	-.10	-.07
	left soleus	-.009	.27
left hand	right soleus	.02	.13
	left soleus	.12	.28

No clear and consistent relationships between reflex amplitudes and performance emerge from these data. In former publications, negative relationships were reported between RTs and reflexes evoked during the foreperiod, but without any consistency with regard to type of analysis (inter- versus intrasubject), leg (involved versus uninvolved) or size of the correlations; the latter appeared always to be slight, however (Requin 1967; Requin and Paillard 1971; Requin, Bonnet and Semjen 1977). The present results thus indicate that reflex changes during foreperiod reflect preparatory state (see also Experiment III), but that they are poor in predicting the resulting performance. This is in accord with the notion referred to in the introduction and with the data presented in experiment IV, indicating that reflexes have a great variability even under apparently identical conditions.

3. Experiment II: early effects on the T-reflex time course

In the second experiment (see Appendix 2 for an extensive description) the short latency reflex increment following the warning signal was the subject of further investigation. The aim was to find out whether stimulus factors contributed solely to the described peak, or whether task factors contributed also. It was found that intensity and modality both influenced the peak: an intense (auditory) stimulus caused a sharp and more pronounced

increase than did a less intense stimulus, while the application of a visual instead of an auditory warning signal caused the peak to arise after a considerable delay. Auditory and visual signals were not matched for subjective intensity, however.
Duration of the (auditory) stimulus affected the T-reflex time course only marginally.

In addition to these results, it appeared that the preparatory process was not confined to the later part of the foreperiod, but was reflected in the T-reflex time course as early as 200 milliseconds after warning signal onset. Clearly, the spinal motor system shows signs of preparatory motor activity earlier than could have been inferred from slow cortical potential, EMG and heart rate studies; these early signs of preparation, however, are parallelled by the first task-related components of the cortical evoked potential (Näätänen and Michie 1979). Presentation of an (auditory) stimulus alone, that is, without a second stimulus and a response to follow, also resulted in an early increase, but with the increase subsiding again after about 300 milliseconds. Such a responsiveness to sound is remarkable, as structures at low levels in the CNS seem to play no role whatsoever in processing of the stimulus.

The question that arises is whether this early increase can be designated an orienting response (OR) and if so, what exactly constitutes the OR: the first peak that arises within a few hundred milliseconds, or the sustained increase thereafter, that occurs when a movement is prepared. The latter could be (part of) an OR, but also the reflection of increased processing requirements associated with a signal stimulus, or indeed increased preparatory activity that is relatively independent of the warning signal. The question as to the orienting function of this early increase cannot be answered, as long as the eliciting conditions with regard to the OR, i.e. whether it is novelty or significance (see Rohrbaugh 1984), are not established.

In surface EMG recordings, short latency increases due to auditory stimulus presentation have also been described. Davis (1948) for instance, reported peaks in the EMG occurring in arm muscles with a latency of about 400 milliseconds; stimuli below 100 dB intensity, however, had no such effect. Gogan (1970) found increases which had a considerable shorter latency (of about 30 milliseconds), even with stimuli of 32 dB intensity; here, recordings were made in unidentified muscles of the arm, neck and face. Rossignol (1975) is the only author known to us reporting short latency EMG responses recorded in the human leg. Stimuli of 114 dB, an intensity high enough to elicit startle, were used by this investigator. Startle responses were found predominantly in

the flexor muscles of the limb and less often in extensors, such as the soleus and gastrocnemius muscles. Thus, we found no evidence that weak stimuli cause increases in EMG activity. The findings corroborate the conviction of Paillard (1955) that reflexes are more apt to signal slight changes in motor output than is the EMG.

In Experiment III, to be reported in the next chapter, combined recordings of both the background EMG and T-reflexes will further illustrate the greater sensitivity of the T-reflex to sound.

4. Experiment III: reflexes and background EMG activity during movement preparation and stimulus anticipation

The third experiment (see Appendix 3 for an extensive description) concerned the solution of some major problems which had arisen from the first and second experiment. First, the aim was to investigate whether the reflex changes occurred prior to a motor response only, as had implicitly been assumed by designating the processes intervening between S1 and S2 as being motor preparatory. It could well be that imposing a mental load on the subject, i.c. instructing him to anticipate a forthcoming stimulus but not to respond to it, would give rise to similar reflex patterns as have been described in chapter 2. This seemed to us not unlikely, as Brunia (1970) documented a T-reflex increase during the performance of a mental (i.e. signal discrimination) task, which could not be explained by the associated motor responses alone (see also Brunia and Boelhouwer in press).

Unfortunately, however, anticipation and preparation are hard to isolate experimentally. Preparation, by its very definition, always involves anticipatory processes, whereas mere anticipation often becomes manifest only by means of a motor reaction. We tried to study anticipation by employing a guessing task introduced by Donchin, Gerbrandt, Leifer and Tucker (1972). According to this task pairs of stimuli were presented to the subject, the interval between the two stimuli being four seconds. The subject's task was to predict the occurrence of the second stimulus, which could appear on the right or the left side of the stimulus display. Predictions were made by pressing one of two keys prior to presentation of the first stimulus. The subjects were rewarded for correct predictions, while no other motor responses than the key-presses were required.

The result was that stimulus anticipation did not cause

the reflex amplitudes to change, except for the short latency peak associated with the first stimulus. There was a difficulty here, in that the mental loads provided by the preparation and anticipation tasks were not necessarily the same. It remains a hypothesis to be rejected, therefore, that T-reflex patterns during a foreperiod reflect preparatory state and not just increased arousal.

The second purpose of the third experiment was to distinguish between simple and choice RT and thus to relate physiology to behavior. As choice RT tasks are known to result in longer RTs and as the differential effect described in Experiment I was held to reflect the selective aspects of preparation, the hypothesis was that the differential effect would be less or absent during a choice RT task. It was decided to record the surface EMG of the soleus muscles also, as it had been found (see the introductory chapter) that subjects sometimes tense their muscles during preparation. The presence of muscle activity would not only impede a correct interpretation of the reflex results, but would possibly also weaken the original argument in favor of the reflex technique, saying that reflexes show changes in motoneuron excitability that cannot be deduced from EMG recordings.

The results showed similar reflex patterns for simple and choice RT tasks, whereas the performance data, i.e. mean RTs, did differ. Again there was a dissociation between physiological measures and behavior, except for the period after the response signal, where reflex increases were more prominent for the involved leg in both types of task. So with regard to the predictive value of the reflexes it can be concluded that this is poor, not only when performance is related to reflexes within and across subjects as was argued when Experiment I was described, but even when the average results of groups of subjects are compared across different RT conditions.

A third interesting finding was that reflex modulation occurred independently of the background EMG. The EMG trace showed no changes at all in either condition. To our knowledge this is the first time that combined recordings of reflexes and background EMG, obtained from the same muscle, have been presented. The results corroborate the old argument in favor of the reflex technique against mere surface EMG recordings, and allow for a further physiological interpretation of the reflex results: when surface EMG is absent and the subject is completely relaxed, it is plausible that phasic reflex changes reflect descending neural activity that acts upon the alpha motoneuron, probably through interneurons, but that remains subthreshold.

There was a problem, however, in that the differential effect did not show up in conditions in which muscle tension in the two legs was prohibited. As in a former experiment by Haagh, Spoeltman, Scheirs and Brunia (1983) the differential effect at the moment of response signal onset was found to be increased when the response relevant muscle was tensed, muscle tension emerged as a factor that could prove to be very important in the understanding of this phenomenon.

Thus a fourth experiment was conceived, in which reflexes were evoked under different degrees of instructed muscle tension.

5. Experiment IV: muscle tension and the T-reflex

In the fourth experiment, T-reflexes were evoked both in and outside a warned RT task while the level of muscle tension was varied by instructing and training the subjects (see Appendix 4 for an extensive description).

When reflexes were recorded during the later part of the foreperiod and the EMG trace was recorded continuously, it appeared that the instruction to tense the involved soleus muscle caused the differential effect to grow larger (and the reflexes in the tensed leg to decrease even below baseline), whereas when both muscles were relaxed reflexes in the two legs remained above baseline and the difference between the two was reduced to a statistically nonsignificant one.

Reflexes were also evoked when the instruction to the subjects was to maintain a specified level of unilateral muscle tension, without any further task involvement. Several low levels of isotonic tension were applied (as assessed by EMG output), relative to each individual's maximal voluntary contraction strength.

It appeared that as tension of the right soleus muscle increased, the difference between the reflexes evoked in the two legs increased also; reflexes in the tensed (right) leg showed the lower values and varied in proportion to the level of tension, whereas reflexes in the relaxed (left) leg showed hardly any changes. Recordings of the activity of the tibialis anterior muscles indicated that some subjects did not tense the right soleus muscle selectively, but activated the ipsilateral tibialis anterior muscle in cocontraction. This, however, was without any effect on the differential effect.

Thus, as the tendency of some subjects to tense their muscles in advance of a motor response had been revealed, it was proposed that the relative reflex depresssion found in

Experiments I and II but not in Experiment III could be explained as being secondary to background muscle tension also. The mechanism responsible for such a reflex decrease need not be neuronal but could instead be a peripheral one, i.e. the increased stiffness of the muscle (and the decreased effectiveness of the tendon tap as a consequence) which is due to muscle contraction. Indirect support for the latter explanation was provided by the fact that two other spinal reflexes, the H-reflex and the first component of the triceps surae stretch reflex, were shown not to be decreased but increased during muscle tension (Gottlieb, Agarwal and Stark 1970; Kearny and Chan 1982). One of the major differences between the latter two reflexes and the tendon jerk seems to consist of the greater sensitivity of the tendon jerk to changes in mechanical properties of the muscle, such as muscle stiffness or slight changes in foot position.

6. Conclusions

In summary, the combined Experiments I-IV allow for the following tentative conclusions with regard to the motor preparatory and movement execution process.

1. The preparatory process, as inferred from reflex and surface EMG recordings, is characterized by at least four consecutive phases: a. a short latency increase in descending activity that is bound to the presentation of stimuli, both auditory an visual. b. a smaller increase immediately following the increase mentioned in a. and persisting until the end of the foreperiod; this increase reflects motor preparatory state. c. the final and large increase accompanying the actual movement (see Haagh, Spoeltman, Scheirs and Brunia 1983) and d. a neuronal inhibition causing agonist muscle release.

2. Spinal motorstructures with a different functional significance might, but need not be affected differentially during foreperiod. Whether involved and noninvolved motor structures are facilitated to an equal extent or whether the involved structures are activated preferentially seems to depend on the subject's response strategy and on the instructions given to the subject with regard to the tensing or relaxing of response relevant muscles.

The combined reflex and surface EMG recordings, as well as evidence obtained from studies employing electrically evoked and stretch reflexes suggests that facilitation is the rule during motor preparation. There is no need to postulate a role for an

active inhibitory process, neither general nor diffuse, except after the foreperiod when the movement has been completed and the soleus muscle is released.

3. The functional significance of the reflex patterns during foreperiod remains unclear. An appealing explanation is that the increased excitability levels were obviously aimed at increasing the response sytem's activity level toward the motor action limit, and thus at increasing response speed. This, however, is unlikely in the light of the absence of any clear relationships between reflex amplitudes and performance, and because of the very generalized reflex pattern that occurred even during preparation of remote responses that required little effort. A possibility that has to be considered is that the reflex patterns described in this thesis are peripheral sequelae of central processes, rather than presettings of the spinal motor circuitry that are necessary for movement.

4. In general, spinal monosynaptic reflexes are able to reveal changes in motoneuron excitability that remain below motor threshold, as was proposed by Paillard (1955). An excitability increase due to stimulus presentation, for instance, was always seen in our experiments, even when the stimulus was weak or without significance. Reflexes also seem to differentiate well between preparatory motor and mere anticipatory activity, whereas the surface EMG does not. Individual or averaged reflex amplitudes, however, have been found to be poor predictors of behavior.

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Summary

SUMMARY

Monosynaptic spinal reflexes, such as the patellar and Achilles tendon reflex, have been known for about a century. They are widely applied as tools in clinical diagnosis. In addition, reflexes were found to be sensitive indicators of mental functioning: it appeared that reflexes were depressed during sleep and that their amplitude was increased during mental tasks, for instance during mental arithmethic and signal discrimination tasks.

In this thesis, Achilles tendon (T) reflexes were employed to test the excitability of the human motor system during preparation of a voluntary movement. During preparation both sensory and motor adjustments take place that facilitate performance; these adjustments, however, are not always easily inferred from observing the subject's behavior, nor from recordings of ongoing physiological processes from the surface of the body.

Therefore, an alternative mode of assessing the activity level of the nervous system was introduced by Paillard (1955). His arguments in favor of the reflex technique instead of mere surface EMG recordings were 1. that reflexes could reveal changes in motoneuron excitability that remained subthreshold to the firing of motoneurons, and 2. that inhibitory influences acting on the motoneuronpool at rest could possibly be detected by this technique. Both arguments have been corroborated in the experiments that are described in this thesis.

In all experiments, Achilles tendon reflexes were evoked at several points in time during the foreperiods of warned reaction time experiments. Movements to be executed were unilateral foot or finger flexions, thus designating the triceps surae muscles as agonists or as irrelevant muscles with regard to the response. The aim was to reveal the time course of preparation at the ultimate neuronal level at which the descending information from brain to muscles could be modified: the lumbo-sacral spinal cord. A further aim was to compare the spinal patterning of activation with recordings of other physiological parameters, such as EEG activity, heart rate, pupillary diameter and brainstem reflexes, that had been reported in the litterature. In all parameters except in heart rate, there was a stimulus bound increase in reactivity, appearing during the first half of the foreperiod. The first increase was followed by a second one toward the end of the foreperiod, this increase

reflecting the intention to move.

In Experiment I, the above pattern was found to be present also in the T-reflex, regardless of whether a foot flexion or a finger flexion served as the response. The latter phenomenon, a similar reflex time course prior to different types of responses, was an important characteristic. It pointed to the generality of the response pattern, as it occurred even in motoneuron pools remote from the responding member and under conditions of low to moderate force and speed demands. For that reason, it could be hypothesized that such changes have to be considered as peripheral sequelae of some central process, rather than as presetting mechanisms which have functional significance with regard to the task at hand.

In contrast, a second characteristic of the reflex time course did appear to be related to function: this was a difference in amplitude of the reflex changes in the response involved and noninvolved legs, the involved leg showing the same temporal pattern as the noninvolved one but deviating less from baseline. The effect was first interpreted as being due to a selective and presynaptic inhibitory mechanism, but in later experiments (Experiments III and IV) another explanation was proposed.

After the foreperiod, there was a large reflex increase reflecting the descending commands for movement initiation and execution. Finally, there was a sharp decline in reactivity, probably reflecting both the poorer impact of the reflex hammer on the tendon and an active neuronal inhibition accompanying muscle release. It appeared that reflexes, either within or across response conditions, were poor predictors of the individuals average performance level.

In Experiment II, the stimulus bound increase at the beginning of the foreperiod was the subject of investigation. It was found that physical aspects of the stimulus influenced the amplitude of the first peak: duration of an auditory stimulus had hardly any effect, as opposed to intensity: a higher intensity resulted in a more pronounced peak. A visual instead of an auditory stimulus gave rise to a peak after a considerable delay: after about 200 msec as compared to about 100 msec with an auditory stimulus. This result was interpreted as a physiological analogon of the immediate arousal efect, known from reaction time research.

Although physical warning signal parameters influenced the reflex time course at the beginning of the foreperiod, they proved to be without any effect on performance. The instruction to respond, on the other hand, did affect the time course of the

early reflex peak. When a reaction time task and a passive listening condition were compared, it appeared that the early reflex pattern during foreperiod showed an increase in two successive or overlapping phases, the first being stimulus and the second being response bound. These results indicated that signs of preparatory motor activity are not necessarily restricted to the second half of the foreperiod.

In Experiment III, a simple and a choice reaction time experiment were carried out. Also, a guessing task was introduced, involving the subject's active attention to and expectancy of a stimulus but not the preparation of a motor response. In this experiment, surface EMG recordings were made to ensure that subjects acted according to instructions, that is, that they remained in a relaxed state during motor preparation.

It appeared that a reflex increase depended on the performance of a motor response, and also that the simple and choice RT tasks yielded similar reflex patterns. The mean reaction times did differ, however. These findings and the results of Experiment I might indicate that spinal motoneuron pools are preset only prior to tasks that involve the final activation of these or other motoneuron pools, but without any clear relationship to the quality of task performance.

Further evidence as to the diffuse nature of these presetting processes at the spinal level was provided by the absence of any difference between the reflex patterns in the involved and noninvolved legs during the simple RT task, a finding that contrasted with the general reflex time course that had been observed in Experiment I. It was argued that the slight tension of response relevant muscles, a phenomenon known to occur in some subjects spontaneously as part of the preparatory process, could have interfered with reflex amplitudes recorded in Experiment I and in other studies not involving surface EMG recordings.

The possible contribution of muscle tension was the subject of investigation in Experiment IV. In this experiment, reflexes were evoked under varying levels of agonist muscle tension, both in and outside a warned reaction time task. It appeared that the differential reflex effect varied in proportion to the level of tension, the difference being absent when subjects were relaxed. It was therefore concluded that the differential effect need not be neuronal but could be interpreted as being secondary to muscle tension.

The general conclusions from the experiments with regard to the spinal preparatory process were thus stated as follows:

- the preparatory and movement execution process is characterized by at least three consecutive phases showing a diffuse increase in descending neural activity: the first is stimulus bound, the second reflects the intention to move and the third phase reflects movement initiation. Finally, there is a fourth phase showing a sharp decrease in excitability (but possibly due to an increase in inhibitory activity), that is not diffuse but confined to the agonist muscle and that reflects muscle release.

- a reflex pattern during foreperiod that is not diffuse but differs for muscles that are differentially involved in the movement can be explained on the basis of a difference in muscle tension, which might, in turn, be considered to be part of the preparatory process.

- the functional significance of the changes in reflex excitability during foreperiod remains unclear, as there were no clear relationships with measures of performance and as the observed reflex patterns occurred even during the preparation of remote movements requiring little effort.

- spinal reflexes are more easily modified by both stimulus presentation and (motor)task instructions than is the surface EMG.

Samenvatting

SAMENVATTING

Monosynaptische, spinale reflexen, zoals de kniepees- en Achillespeesreflex (T-reflex), zijn sinds ruim een eeuw bekend. Ze worden vooral toegepast voor het stellen van diagnoses in de klinische praktijk.

Daarnaast is gebleken dat reflexen informatie kunnen verschaffen over het alertheidsniveau van mensen; de amplitudo van dit type reflexen is bijvoorbeeld lager tijdens slaap en hoger tijdens sommige vormen van mentale belasting.

In dit proefschrift is onderzoek gedaan met T-reflexen. Deze reflexen werden opgeroepen tijdens de voorbereiding op de uitvoering van een vrijwillige beweging, om aan de hand van amplitudo-veranderingen van de reflex uitspraken te kunnen doen over de prikkelbaarheid van motorische strukturen in het ruggemerg. Bewegingsvoorbereiding is een veelzijdig proces, dat ook voor de psychologie van belang is omdat de meeste vormen van psychisch funktioneren uiteindelijk slechts via motorische responsen bestudeerd kunnen worden. Daarbij is het niet voldoende om alleen op het observeerbare gedrag te letten, of af te gaan op veranderingen in fysiologische maten die aan de oppervlakte van het lichaam zijn geregistreerd. Minuskule veranderingen onttrekken zich dan wellicht aan onze aandacht.

Paillard (1955) was degene die met dit doel de reflextechniek introduceerde. Zijn argumenten waren, dat met deze techniek ook veranderingen in prikkelbaarheid die onder de vuurdrempel van motoneuronen blijven, zichtbaar zouden kunnen worden gemaakt. En verder, dat remmende invloeden op de motoneuronen in een daling van de reflex-amplitudo's tot uiting zouden kunnen komen. Beide argumenten hebben in dit proefschrift steun gekregen.

In de vier experimenten die in dit proefschrift beschreven worden, zijn steeds reflexen opgeroepen in beide benen, op verschillende vaste tijdstippen tijdens voorperiodes van een reaktietijd-experiment. De voorperiodes hadden een duur van vier sekonden. Een dergelijke voorperiode werd steeds afgesloten met een reaktie-signaal, waarop zo snel mogelijk een beweging moest volgen. Bewegingen konden plantair-flexies van de voet zijn, maar ook het indrukken van een knop met een van beide wijsvingers. Zo konden de reflexveranderingen zowel een beeld geven van strukturen die funktioneel bij de beweging waren betrokken, als ook, in het geval van T-reflexen voorafgaand aan vingerbewegingen, van strukturen die niet bij de beweging

waren betrokken.

Een kommando om te bewegen wordt in het zenuwstelsel gegenereerd in de hersenen en bereikt via meerdere schakelstations de spieren. Het doel van het onderzoek was het verloop van het preparatieproces te bestuderen op het laagste neuronale niveau waarop nog veranderingen mogelijk zijn, namelijk ter hoogte van het lumbo-sacrale ruggemerg. Daar liggen namelijk de cellichamen van de alpha-motoneuronen die de kuitspieren innerveren. Ook zou op deze wijze een vergelijking kunnen worden gemaakt met bijvoorbeeld veranderingen in hersen-aktiviteit, spierspanning of anderssoortige reflexen, waarover in de literatuur wordt gerapporteerd. Vrijwel altijd is er in die laatste parameters sprake van twee achtereenvolgende aktiviteits-toenames tijdens de voorperiode, de eerste gekoppeld aan presentatie van het waarschuwingssignaal (S1) en de tweede waarschijnlijk verband houdend met het motorische preparatie-proces.

In Experiment I werd eenzelfde patroon gevonden als hierboven beschreven, zowel voorafgaand aan voet- als aan vingerbewegingen. Dit laatste wees op het algemene karakter van de reflexveranderingen, die kennelijk ook optreden wanneer bewegingen moeten worden uitgevoerd die weinig inspanning vereisen of die geschieden door spieren die ver af liggen van het reflexcircuit dat getest wordt. Misschien duidt dit op de afwezigheid van een funktionele relatie tussen reflexveranderingen en motorpreparatie, een idee dat ook door de geringe samenhang tussen reflexgrootte en prestatiematen onderschreven wordt. Echter, een aspekt van de reflexkurve lijkt duidelijk funktioneel bepaald: het verschil in reflexen tussen het bij de reaktie betrokken en het niet bij de reaktie betrokken been. In het betrokken been waren de reflexen steeds lager, terwijl het verloop in de tijd voor beide benen gelijk was. Dit verschijnsel werd aanvankelijk als een vorm van presynaptische inhibitie geinterpreteerd, maar later (Experiment III en IV) werd een andere verklaring voorgesteld.

Na de voorperiode was er een opvallende en snelle reflexverhoging, die de aanzet tot de uitvoering van de beweging weerspiegelde. Tenslotte daalden de reflexen na de beweging tot het nul-niveau; een gevolg van het slechtere kontakt tussen de reflex-hamer en de Achilles-pees, maar waarschijnlijk ook van een aktief neuronaal inhibitie-proces dat bij het ontspannen van een spier na een kontraktie gewoonlijk een rol speelt.

De vroege piek in de reflexen was het onderwerp van onderzoek in Experiment II. Physieke kenmerken van de waarschuwingsstimulus bleken de amplitudo van deze piek te

beinvloeden: stimulusduur had nauwelijks effekt, maar intensiteit van de stimulus wel. Een grotere intensiteit leverde een grotere amplitudo op. Een visuele in plaats van een auditieve stimulus bleek eerst na een latentietijd van ongeveer 200 msec een reflex-verhoging op te leveren. Een latentietijd die twee keer zo lang was als die bij een auditief signaal en die wellicht vergelijkbaar is met het algemene vertragende effekt dat visuele signalen ook op reaktietijden blijken te hebben.

De physieke stimulus-kenmerken hadden geen effekt op de reaktietijd. Wel bleek de reflexkurve aan het begin van de voorperiode te worden beinvloed door de instruktie om al dan niet na de voorperiode een beweging uit te voeren. Voorbereiding op een beweging had een langer durende reflex-toename tot gevolg. Hieruit blijkt dat bewegingsvoorbereiding niet slechts in het laatste gedeelte van de voorperiode, maar ook al vlak na S1 tot uiting komt.

In Experiment III moesten de proefpersonen een enkelvoudige en een keuze-reaktietijdtaak uitvoeren. Ook moesten ze aan een voorspellingstaak meedoen, waarbij slechts aandacht voor een te verschijnen stimulus en niet de uitvoering van een beweging aan de orde was. In dit experiment werd het oppervlakte-EMG van de kuitspieren geregistreerd om er zeker van te kunnen zijn dat de proefpersonen de hen opgedragen taken volbrachten zonder tijdens de voorperiode de kuitspieren aan te spannen.

Uit de resultaten bleek dat een reflextoename slechts tijdens bewegingsvoorbereiding optrad, en niet tijdens het alleen maar anticiperen op een stimulus. Ook bleken er geen verschillen te zijn tussen de reflexpatronen in de twee reaktietijdtaken, maar wel, zoals gewoonlijk, tussen de reaktietijden zelf. Deze bevindingen en die uit Experiment I suggereren dat de prikkelbaarheid van motoneuronpools tijdens het verrichten van psychologische taken alleen verandert wanneer de taak onder meer uit een motorische respons bestaat; en ook dan is er geen verband tussen de grootte van de veranderingen en de snelheid van de respons of de rol die de motoneuronpools lijken te spelen bij het uitvoeren van de respons.

Dat de reflexveranderingen tijdens een voorperiode algemeen van karakter zijn, dat wil zeggen onafhankelijk van de vraag of de respons met de vinger of de voet moet worden uitgevoerd, was al in Experiment I gebleken. In Experiment III werd dit weinig specifieke karakter nog eens benadrukt door de afwezigheid van enig verschil tusen de reflexpatronen in het betrokken en niet-betrokken been, hetgeen een kontrast vormde met de gegevens uit Experiment I. Als mogelijke verklaring werd aangevoerd dat proefpersonen in experimenten waarin een verschil

gevonden was wellicht in geringe mate hun spieren hadden aangespannen, met een relatieve reflexdaling als gevolg. Het is namelijk bekend dat proefpersonen soms, tenzij hun dat duidelijk verboden wordt, spontaan hun spieren spannen teneinde sneller te kunnen reageren.

De mogelijke rol van achtergrond-spierspanning bij reflex-veranderingen was het onderwerp van studie in Experiment IV. In dit laatste experiment werden reflexen opgeroepen tijdens verschillende maten van spierspanning. Dit gebeurde in een enkelvoudige reaktietijdtaak, maar ook bij het handhaven van een bepaald spanningsniveau zonder meer. De resultaten maakten duidelijk dat het verschil in reflexamplitudo's tussen rechter- en linkerkant (het betrokken en niet-betrokken been) recht evenredig was met de mate van achtergrond-spierspanning. De konklusie was dat het verschil tussen de reflexen in het linker- en rechterbeen niet de weerspiegeling van onder meer een selektief remmend mechanisme hoefde te zijn, maar dat het ook gezien kan worden als een bijverschijnsel van het selektief aanspannen van spieren, een vaak optredend element in het proces van bewegingsvoorbereiding.

De algemene konklusies van de vier experimenten kunnen als volgt worden weergegeven:

-bewegingsvoorbereiding en -uitvoering kan worden gekenmerkt door minstens drie opeenvolgende fasen die een toename van algemene descenderende aktiviteit te zien geven; de eerste fase is stimulus-gebonden, de tweede weerspiegelt de intentie om te bewegen en de derde fase weerspiegelt de commando's die de spieren moeten doen samentrekken. Tenslotte is er een vierde fase die een plotselinge afname van de prikkelbaarheid laat zien. Deze fase is niet algemeen, wat wil zeggen dat hij slechts optreedt in de spier die ten aanzien van de beweging als agonist fungeerde. Waarschijnlijk is het een weerspiegeling van een remmend neuronaal proces.

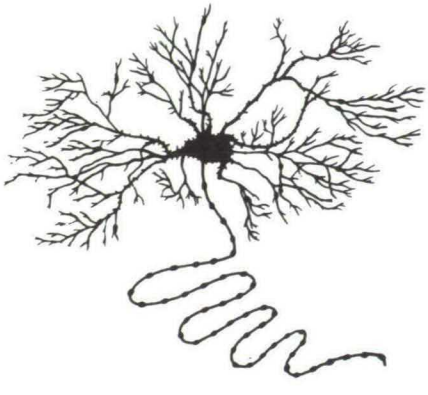
-een reflexpatroon tijdens de voorperiode dat selektief is, dat wil zeggen verschillend voor wel en niet bij de reaktie betrokken neuronale circuits, kan verklaard worden door selektieve spierspanning. Een dergelijke selektieve spierspanning kan gezien worden als een normaal onderdeel van bewegingsvoorbereiding.

-de funktionele betekenis van de hier bestudeerde reflexveranderingen tijdens een voorperiode blijft onduidelijk. Er waren immers geen relaties tussen reflexgrootte en prestatiematen, en de reflexpatronen voorafgaand aan weinig energie eisende vingerbewegingen waren niet anders dan die

voorafgaand aan plantairflexies van de voet.

-de grootte van spinale reflexen is gevoeliger voor de aanbieding van stimuli en voor instrukties die de uitvoering van een motorische taak behelzen, dan het oppervlakte-EMG.

Appendices



Appendix 1.

Changes of Achilles tendon reflexes during a fixed foreperiod of four seconds

Changes of Achilles Tendon Reflex Amplitudes During a Fixed Foreperiod of Four Seconds

ABSTRACT

Preparation for a voluntary foot or finger response was studied by evoking Achilles tendon (T) reflexes. Reflexes were evoked simultaneously in both legs at 13 points between 100 and 4300 msec after the warning signal. With this paradigm, the time course of changes in reflex amplitudes related to preparatory processes could be measured simultaneously in the leg involved in the response and in the uninvolved leg. Immediately following the warning stimulus, the reflex amplitudes increased in both involved and non-involved muscles, presumably reflecting a general non-specific arousal. During the second half of the foreperiod, reflex amplitudes in non-involved muscles remained elevated, perhaps reflecting a general activation of the motor system, but returned to baseline in the involved muscles. It is hypothesized that the consistently smaller reflex amplitudes in the involved leg during the entire ISI reflect a presynaptic inhibition of the Ia afferents to the motoneurons involved in the response. Following the response stimulus, reflex amplitudes increased in both involved and non-involved muscles, although in the former at an earlier point and to a greater extent. It is suggested that this increase following the response stimulus is a manifestation of the transition from motor preparation to response execution.

DESCRIPTORS: Achilles tendon reflex, Motor preparation, Response Intention, Reaction time.

The execution of a voluntary movement implies an activation of spinal motoneurons by means of a supraspinal command. In a reaction time (RT) experiment such a command can be triggered by an imperative stimulus. RT decreases when a warning signal (WS), followed by a foreperiod of fixed duration, is employed. This method allows the subject to anticipate the response. Between the WS and the response signal (RS) several physiological changes can be recorded, which might be related to response intention. Lacey and Lacey (1970, 1974) interpreted part of the deceleration in heart rate around the RS in these terms. Loveless and Sanford (1974), Rohrbaugh, Syndulko, and Lindsley (1976), and Gaillard (1978) emphasized in their contingent negative variation (CNV) studies the relationship between the amplitude of the late wave and the RT. Changes in the excitability of certain reflex circuits at the spinal level also seem to be related to preparation for a response (Requin, Bonnet, & Semjen, 1977).

This work is supported by the Dutch Organization for the Advancement of Basic Research ZWO (Grant 78–384).

The assistance of Ed van den Bosch in programming is gratefully acknowledged.

Effects of preparatory processes on spinal level responses can be studied by evoking during a foreperiod a reflex that engages the same motoneuron pool that is involved in a voluntary movement. The movement we investigated was a plantar flexion of either the right or left foot, for which a contraction of the triceps surae muscle had to be made.

Two segmental monosynaptic reflexes can be evoked over the same motoneuron pool involved in the plantar flexion: the Achilles tendon (T) reflex and the Hoffmann (H) reflex. If a tap on the Achilles tendon is given, the muscle spindle is stretched. This produces an afferent volley over Ia fibres to the alpha motoneurons which, after discharge of these neurons, makes the muscle contract. Since the sensitivity of the muscle spindle is determined by fusimotor neuron activity, the T reflex amplitudes reflect, among other things, changes in the excitability of both alpha and fusimotor neurons. In H reflexes, on the other hand, Ia fibres are electrically stimulated, so the muscle spindle is bypassed and the fusimotor neurons play no role. The Ia afferent fibres of both H and T reflexes are controlled by presynaptic inhibition. Thus, H and T reflex amplitudes are an

index of alpha motoneuron output, which itself is the result of several processes at different positions in the reflex circuit.

If reflexes are evoked simultaneously in both legs during the foreperiod of a RT experiment, but the voluntary response is executed for one leg, it is possible to study the time course of the changes in the spinal reflex circuits and to differentiate response components which are related to preparatory processes. In case of similar changes in both legs, the conclusion that these changes are not specific would seem warranted. However, a differential response from the two legs might indicate involvement of separate neural elements in the preparatory process.

Requin (1969) studied changes in reflex amplitudes during a fixed foreperiod of 1 sec. He found a decrease in T and H reflex amplitudes toward the end of the foreperiod, when subjects were asked to respond with a plantar flexion of the right foot. This decrease was present only in the leg that had to respond. Furthermore, only a slight difference between the time courses of H and T reflex changes was found, although the decrease in the H reflex amplitude was more pronounced. In another experiment Requin (1965) found an increase in EMG activity during the foreperiod in the muscle which was going to respond. This points to an increase in the output of the motoneurons whereas in a similar situation the reflexes evoked via the same motoneuron pool were reduced. As an explanation of this apparent discrepancy he suggested a presynaptic inhibition of the Ia fibres that were electrically stimulated to evoke the reflex. Its function could be to selectively prevent the involved motoneuron pool from being disturbed by peripheral influences.

Since CNV studies (Loveless & Sanford, 1974; Rohrbaugh et al, 1976; Gaillard, 1978), in which longer foreperiods were used, revealed two slow negative waves, the late wave being selectively related to the setting for the response, Brunia and Vuister (1979) investigated H reflex changes during a foreperiod of 4 sec. Using the same response as Requin (a plantar flexion of either the right or the left foot) the authors did not find a decrease below baseline in H reflex amplitudes. Rather there was a non-specific increase shortly after the WS, followed by a decrease and a second non-specific increase nearer the presentation of the RS. In general, amplitudes in the involved leg tended to be slightly smaller than in the non-involved leg, but the difference was not significant. In a former study Brunia (1979) reported that as the foreperiod progressed, T reflex amplitudes increased more in the involved than in the non-involved leg. However, the peak-to-peak detector employed in that study did not differentiate well between a T reflex amplitude and proximate EMG bursts accompanying the voluntary movement. Therefore T reflexes were investigated again during a 4-sec foreperiod, with the expectation that the time course of the T reflex would be comparable to that of the H reflexes.

In addition to the foreperiod effects several authors reported changes in excitability of motoneurons after the response signal. A facilitation of the T reflex as well as the H reflex at 50–80 msec prior to a voluntary contraction of the triceps surae muscle has been reported (Pierrot-Deseilligny, Lacert, & Cathala, 1971; Michie, Clarke, Sinden, & Glue, 1975, 1976; Kots, 1977). These findings suggest that a third increase in T reflex amplitude should be found shortly after the presentation of the RS. In order to study the transition of T reflex amplitudes from the second to the third increase, T reflexes were evoked shortly after the RS as well as during the foreperiod.

Method

Subjects and Apparatus

Eighty subjects, 53 males and 27 females, participated in the experiment. All subjects indicated that they preferentially used their right hand and foot in most of the items of a modified version of the Edinburgh Inventory (Oldfield, 1971). The total range of age was 18–37 yrs with a mean of 22.4 yrs.

Subjects were seated comfortably in a specially designed chair, placed in a dimly illuminated, soundproof and electrically shielded room, with their feet strapped to a footplate. The knees were positioned in approximately 120° of flexion while the ankle was set at 90°. T reflexes were evoked in both legs simultaneously by means of two Brüel and Kjaer 4809 vibration exciters, which were directed at a right angle to the Achilles tendon at the level of the lateral malleolus. The vibration exciters were triggered by a 9-msec rectangular pulse of variable amplitude, produced by two Brüel and Kjaer 2706 power amplifiers. A red LED display (9 cm^2, 200 cd/m^2) was placed at eye level 1.5 m in front of the subject. This visual stimulus served as the RS (duration: 50 msec). A buzzer placed behind the subject was used as the WS (intensity: 80dB(A), duration: 100 msec, rise/fall time: 20/20 msec, total frequency range: 100–5000 Hz). A train of three 50-msec tones with 550-msec intervals was produced by means of a sonalert (2900 Hz, 75dB(A)), to provide immediate feedback to the subject whenever an interval of 400 msec after the RS had elapsed without the occurrence of a response. Experimental procedures and RT-data acquisition were accomplished by means of a DEC Lab 8/e computer.

The electromyographic response was recorded via two Ag-AgCl surface electrodes attached 4 cm apart on the distal part of each soleus muscle. The signals were amplified by Hellige EE preamplifiers (−3dB bandwith: 5.3–1000 Hz) and recorded on magnetic tape (Hewlett & Packard 3960; bandwith: 0–312 Hz). A/D conversion and

measurement of the peak-to-peak amplitudes of the reflexes were accomplished by means of a DEC PDP 11/10 computer.

Procedure and Data Analysis

Four groups were run. In the first two groups the response consisted of closing a microswitch positioned under the footplate, by making a plantar flexion with either the left (I) or right (II) foot. As a control, additional groups were run in which pressing a button mounted in the chair arms with either the left (III) or right (IV) index finger was the required response.

Each foreperiod of 4 sec was followed by an ITI of 16 sec. Reflexes were evoked in a pseudorandom order once during the foreperiod or shortly after the RS, 10 times at each of 13 different temporal measuring points: at 100, 200, 2000, 3500, 3700, 3800, 3900, 4000, 4100, 4150, 4200, 4250 and 4300 msec after the WS. During each ITI a control reflex was evoked pseudorandomly at 6, 8 or 10 sec after the RS. The ITI data were averaged per subject. Mean reflex amplitudes at each of the 13 different measuring points were calculated per subject and expressed as a percentage of the individual average amplitude level during the ITI. The individual percentage scores were used for statistical analysis, and the overall averaged scores were used for the illustrations. Before the start of the experimental session subjects were given 20–30 practice trials. During these trials the experimenter adjusted the tendon tap intensity such that peak-to-peak T reflex amplitudes in the two legs were about equal.

Prior to averaging, reflex amplitudes from trials with premature responses (RT<100 msec) were excluded. If this resulted in less than 7 observations at a given temporal measuring point for a particular subject, all data from that subject were discarded from further analysis. Because of this selection procedure 19 subjects remained in group I, 17 subjects in group II. In the control groups III and IV data of all 40 subjects could be used.

Results

Tendon Reflexes

It was hypothesized that the time course of T reflex amplitudes during and after the foreperiod would show three successive increases. Therefore three separate S(A×B)×C×D Analyses of Variance (ANOVAs) were carried out: one on the reflex data of the first half of the foreperiod (100–2000 msec), one on the data at the end of the foreperiod (3500–3900 msec), and one on the data of the period shortly after the RS (4000–4300 msec). Missing data were calculated by a least squares estimation.

The factors included the between-subjects variables of Responding Member (foot vs finger) and Response Side (left vs right), the within-subjects factors were Laterality (involved vs non-involved or ipsilateral vs contralateral to response side) and Temporal Measuring Points.

In order to compare percentage scores between the left and right legs, baseline levels should be of comparable magnitude. Therefore mean ITI levels were calculated. There were no significant differences in these values between legs ($t_{dep.} < 1.13$, for all groups)[1].

The mean relative amplitudes are depicted in Figures 1 and 2 (left and right foot responses) and Figures 3 and 4 (left and right finger responses).

[1]The .01 level of significance was utilized in all statistical tests, unless stated otherwise.

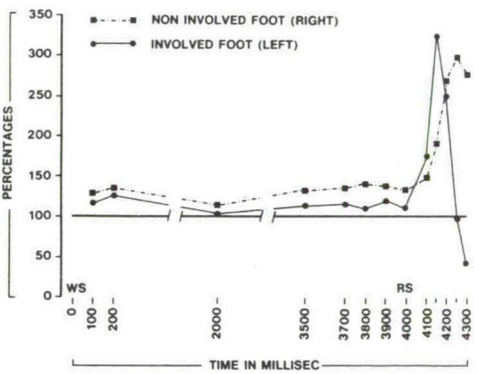


Figure 1. Group I, left foot response (n = 19). Relative amplitudes of Achilles tendon reflexes evoked during and after a 4-sec foreperiod in the involved as well as in the non-involved leg. Mean amplitude of reflexes evoked during the intertrial interval was taken as the 100% level.

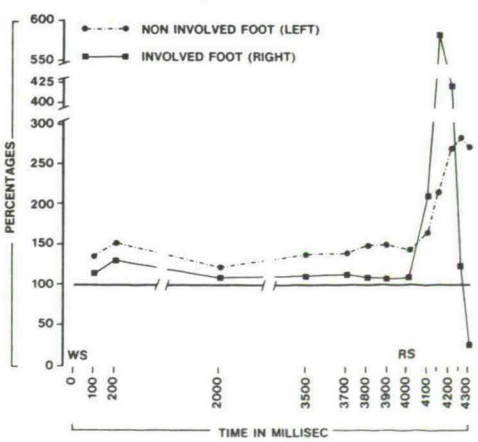


Figure 2. Group II, right foot response (n = 17). Relative amplitudes of Achilles tendon reflexes evoked during and after a 4-sec foreperiod in the involved as well as in the non-involved leg. Mean amplitude of reflexes evoked during the intertrial interval was taken as the 100% level.

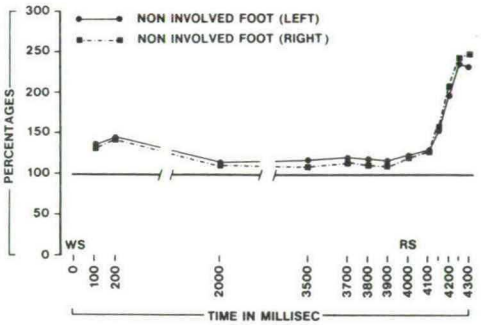


Figure 3. Group III, left finger response (n = 20). Relative amplitudes of Achilles tendon reflexes evoked during and after a 4-sec foreperiod in the left and right legs, both not involved in the response. Mean amplitude of reflexes evoked during the intertrial interval was taken as the 100% level.

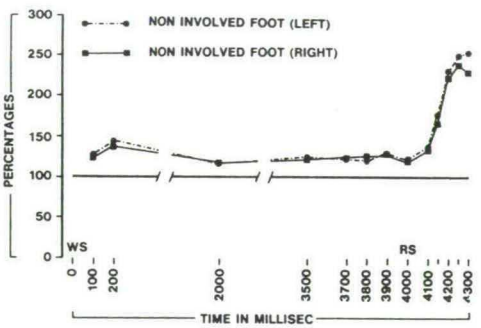


Figure 4. Group IV, right finger response (n = 20). Relative amplitudes of Achilles tendon reflexes evoked during and after a 4-sec foreperiod in the left and right legs, both not involved in the response. Mean amplitude of reflexes evoked during the intertrial interval was taken as the 100% level.

There are significant main effects for Laterality during the foreperiod, and for Temporal Measuring Points in the first half of the foreperiod and the period after the RS (see Table 1). The interaction effect of Laterality × Responding Member indicates a difference between the two legs during the foreperiod, dependent on whether a finger or a foot flexion was the required response. The Temporal Measuring Points effect in the first half of the foreperiod indicates a relative peak in reflex amplitudes at 200 msec. A Gabriel *a posteriori* test reveals that reflexes at 100 msec are smaller than at 200 msec ($F(2/144) = 7.57$) and reflexes at 200 msec are larger than at 2000 msec ($F(2/144) = 35.84$). After the foreperiod there are significant interaction effects of Temporal Measuring Points × all other factors. Thus, the time course after the RS is different for foot and finger responses, for the involved and non-involved leg responses, and for left vs right reactions. Differences in time course between the involved and non-involved leg reactions and between the left and right side reactions depend on the responding member. This is shown by the Responding Member × Response Side × Temporal Measuring Points interaction and the Responding Member × Laterality × Temporal Measuring Points interaction.

To elucidate the differences between the experimental and the control groups as revealed by the interaction effects with factor A (Responding Member), three additional ANOVAs were carried out on the reflex-data for the foot and finger responses separately (see Table 2). Significant differences between the two legs during the foreperiod appear to be present in the foot response groups only (main effect of Laterality), while the Temporal Measuring Points main effects are found in the first half of the foreperiod as well as after the RS for both foot and finger responses. However, the time course after the RS is different for involved and non-involved muscles only when foot movements are considered (interaction effect of Laterality × Temporal Measuring Points). Furthermore, the difference in time course between involved and non-involved muscles after the RS is larger with a right foot response than with a left foot response (interaction effect of Response Side × Temporal Measuring Points).

A separate S(A)×B×C ANOVA on the temporal measuring points at 4000–4100 msec in groups I and II reveals that the increase in amplitude from the RS to 100 msec later is larger in the involved than in the non-involved leg (interaction effect of Laterality × Temporal Measuring Points: $F(1/34) = 14.12$).

When subjects had to respond with their left or right foot, reflex amplitudes at 2000 msec are significantly smaller than amplitudes at 3500 msec in the non-involved leg (Wilcoxon matched pairs signed ranks test, two tailed: $N = 19$, $T = 32$, $p < .01$ (left foot response), and $N = 17$, $T = 35$, $p < .05$ (right foot response)). No such difference is present in the involved leg. In groups III and IV when a finger flexion served as the response, this difference is not found either.

With the exception of amplitudes of reflexes evoked in the involved right or left leg from 2000 to 4000 msec after the WS, relative reflex amplitudes are significantly greater than the ITI baseline in all groups (t-test on means, σ assumed unknown: $t > 3.4$ in all tests).

As is shown in Figures 1 and 2, reflex amplitudes after the RS in the involved leg increase to a much greater extent with a right foot response than with a left foot response. However, the corresponding F ratio (of the interaction effect of Response Side ×

TABLE 1

Summary of overall ANOVAs (S(A×B)×C×D), on two successive parts of the foreperiod (100–2000, 3500–3900) and the period shortly after the RS (4000–4300)

Source	100–2000		3500–3900		4000–4300	
	df	*F*	*df*	*F*	*df*	*F*
A (responding member)	1/72	1.53	1/72	.89	1/72	2.48
B (response side)	1/72	.35	1/72	.88	1/72	2.01
C (laterality)	1/72	12.37*	1/72	9.72*	1/72	1.49
D (temporal measuring points)	2/144	35.92*	3/216	1.86	5/360	44.63*
A×B	1/72	.74	1/72	.61	1/72	1.16
A×C	1/72	12.34*	1/72	18.77*	1/72	.30
A×D	2/144	.27	3/216	.41	5/360	32.70*
B×C	1/72	1.78	1/72	1.13	1/72	2.67
B×D	2/144	.51	3/216	.67	5/360	3.84*
C×D	2/144	.32	3/216	1.27	5/360	31.64*
A×B×C	1/72	.39	1/72	.55	1/72	3.57
A×B×D	2/144	.31	3/216	.87	5/360	3.43*
A×C×D	2/144	.32	3/216	2.43	5/360	32.92*
B×C×D	2/144	1.07	3/216	.72	5/360	2.50
A×B×C×D	2/144	.01	3/216	1.46	5/360	3.33*

*Significant effects.

TABLE 2

Summary of ANOVAs on data from foot and finger responses separately (S(A)×B×C)

Source	100–2000				3500–3900				4000–4300			
	foot		finger		foot		finger		foot		finger	
	df	*F*	*df*	*F*	*df*	*F*	*df*	*F*	*df*	*F*	*df*	*F*
A (response side)	1/34	1.58	1/38	.03	1/34	.01	1/38	1.87	1/34	1.93	1/38	.27
B (laterality)	1/34	25.18*	1/38	.02	1/34	17.54*	1/38	1.11	1/34	.93	1/38	.62
C (temporal measuring points)	2/68	11.62*	2/76	27.29*	3/102	1.23	3/114	.93	5/170	29.36*	5/190	81.90*
A×B	1/34	1.55	1/38	.64	1/34	.90	1/38	.53	1/34	3.77	1/38	.04
A×C	2/68	.38	2/76	.44	3/102	.10	3/114	1.95	5/170	3.98*	5/190	.69
B×C	2/68	.17	2/76	.78	3/102	2.65	3/114	.37	5/170	32.04*	5/190	1.04
A×B×C	2/68	.42	2/76	.87	3/102	1.23	3/114	.80	5/170	2.90	5/190	.09

*Significant effects.

Laterality × Temporal Measuring Points, see Table 2) fails to reach the critical value, although it does exceed the .02 level of significance.

The increase in reflex amplitudes that accompanies preparation for a finger movement is identical on both sides, and comparable to the time course on the non-involved side when foot movements serve as the response. However, the mean increase in amplitude is about 25% less.

Reaction Time

Median RTs (excluding premature responses) depend on the kind of movement to be made. Left foot: 310 msec, right foot: 290 msec, left hand: 230 msec, right hand: 230 msec.

Discussion

The increase in T reflex amplitudes shortly after the WS was found in all four groups, i.e. prior to foot and finger movements. A similar increase in H reflex amplitudes during a 1-sec foreperiod was reported by Requin et al. (1977) and during a 4-sec foreperiod by Brunia and Vuister (1979), independent of the kind of response. In a 3-sec foreperiod, Boelhouwer (1979) found an increase in the first component of the blink reflex shortly after the WS.

His subjects had to respond with a finger flexion or an eye closure. These findings suggest that the early increase in reflex amplitudes recorded in the foreperiod of RT experiments is not associated with the setting for a specific response. It might well be related to the WS itself, since it is known that the mere presentation of an auditory stimulus results in increased amplitudes of reflexes, evoked shortly after that stimulus. This has been reported for the knee jerk (Beale, 1971; Davis & Beaton, 1968), the first component of the blink reflex (Sanes & Ison, 1979), and the H reflex (Rossignol & Melvill-Jones, 1976). Because Davis and Beaton (1968) reported a greater increase following a more intense tone, it can be hypothesized that the early increase is a function of stimulus parameters of the WS. However, variables other than stimulus parameters influence the early increase as well. Data from our institute show a larger increase in T reflex amplitudes after the presentation of the WS if the probability of the occurrence of the RS 4 sec later is less than 1 (Haagh, Note 1). Furthermore, other studies suggest that the latency of the early increase is related to foreperiod duration. An increase in latency when extending the foreperiod from 300 msec to 700 msec was reported by Semjen, Bonnet, and Requin (1973).

Requin et al. (1977) found that the early increase reached a maximum at 100 msec after the WS. In the present study with a 4-sec instead of a 1-sec foreperiod, the early increase reaches a maximum at 200 msec after the WS. This value was also found in a previous study (Brunia & Vuister, 1979), in which additional measuring points were used. Thus, although the early increase is largely determined by stimulus parameters of the WS, it also seems to be influenced by aspects of the preparatory process not related to the execution of a specific response. Therefore we attribute these non-specific changes in the excitability of the reflex circuits to a general arousal.

After an initial increase, reflex amplitudes subsided somewhat, but remained significantly larger than the baseline in the non-involved muscles. The fact that this was found before both foot and finger movements underscores the non-specific nature of this amplitude enhancement during the preparatory period. It looks as if the only muscle in which no indication of presetting processes is present, is the involved muscle. However, there is reason to doubt this conclusion, since Brunia and Vingerhoets (1980) found a systematic increase in EMG activity in the calf muscles of the involved leg during a 4-sec foreperiod. These results and the similar findings of Requin (1965) suggest a presynaptic inhibition, which selectively concerns the Ia afferents to the motoneurons involved in the response. In other words, this might reflect a first specific element in the preparatory process, present from the beginning of the foreperiod.

Our T reflex results show both similarities and discrepancies with H reflex studies. In agreement with the present data, Brunia and Vuister (1979) found H reflex amplitudes which were larger during the foreperiod than during the ITI, both in involved and non-involved muscles. Although the H reflex amplitudes generally did not show the difference between legs that was found for T reflexes, they tended to be smaller in the involved leg during the first second of the foreperiod. Furthermore they were smaller at 1000 msec after the WS than during the early increase, prior to both finger and foot movements. This is in agreement with the data of Requin et al. (1977). Contrary to these authors, we did not find the decrease below baseline. Although we cannot explain this difference, it might be pointed out that in other papers H reflex amplitudes were reported to remain above baseline during a 2-sec foreperiod as well (Papakostopoulos & Cooper, 1973). Apart from the baseline, however, the data of Requin et al. (1977) seem compatible with the first second of our H reflex study and with the present data, though the interpretation is different. Requin et al. (1977) suggested that a widespread inhibition might be present in the spinal cord during a foreperiod of 1 sec, presumably of presynaptic nature. This would imply a process that lacks selectivity. In contrast, we think that our T reflex data point to a more specific mechanism which could be a presynaptic inhibition of the Ia afferents to the involved motoneurons. The interpretation of the difference in H and T reflex time courses during the last 3 sec of the foreperiod can be clarified by further experiments, in which both reflexes are evoked in one session.

Following the RS, reflex amplitudes increased in both involved and non-involved muscles, but in a different way. Several factors might play a role here, related to the time course of changes in motor organization before the response is given. Shortly after the RS, reflexes evoked in involved muscles become larger than in non-involved muscles. Michie et al. (1976) reported an increase in T and H reflex amplitudes prior to the onset of the EMG. With about the same paradigm, Kots (1977) found a similar increase in H reflex amplitudes. Our findings corroborate these data. This increase could be part of a presetting process which selectively concerns the muscle that is going to respond. However, in our study EMG was not recorded, so it is not certain that the amplitude increase takes place prior to EMG onset.

The larger reflex amplitudes in involved right than in involved left muscles at 150 msec after the RS suggest the influence of foot preference. The systematic decrease in reflex amplitudes in involved muscles from 200 msec after the RS is presumably artifactual, reflecting the poorer contact of hammer and tendon because of the beginning of the muscle contraction. After the RS reflex amplitudes in non-involved muscles show a nearly identical time course, with a less steep but rather pronounced increase before both finger and foot movements.

It is not possible to determine whether the increase after the RS is caused by facilitation or disinhibition, nor from which source(s) in the CNS it originates. However, it is plausible that the peak in the involved muscle is caused by a facilitation from the pyramidal tract neurons in the contralateral hemisphere. The motor potential in the EEG is considered to reflect the activation of the precentral motor cortex, while generating the pyramidal tract volley (Deecke, Grözinger, & Kornhuber, 1976). This potential is present in the hemisphere contralateral to the movement side from 60 msec prior to the moment the first spikes in the EMG appear (Deecke, Eisinger, & Kornhuber, 1980). Since it is assumed that the pyramidal tract activity is a unilateral phenomenon, it was hypothesized that the motor potential might be related to the selective increase in reflex amplitudes after the RS (Brunia, 1980). Besides, it is very likely that part of the increase in reflex amplitudes in non-involved muscles, and perhaps to a comparable degree in the involved muscle as well, is due to the presentation of the RS. The RS triggers a non-selective activation, which results in a generalized increase in motoneuron excitability along the spinal cord, while the setting for the response is manifest as an extra and steeper increase on the involved side.

Reflex amplitudes in non-involved muscles preceding foot movements were somewhat larger than those preceding finger movements. This extra increase might be caused by the supra spinal setting of several motoneuron pools at the lumbar level as a first step in the selective activation, which is followed by the final selection of the motoneuron pool involved in the response.

Summarizing, we think that by using reflexes in a warned RT experiment, it is possible to record a combination of processes. The WS triggers a general arousal, indicated by an increase in reflex amplitudes in muscles involved and not involved in the response. This is superimposed upon a relative presynaptic inhibition of the Ia afferents to the motoneurons involved in the response. This inhibition is present during the total length of the foreperiod, together with a facilitation of the non-involved motoneurons. The presentation of the RS is followed by the selective activation of the motoneurons to execute the response.

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Appendix 2.

Effects of stimulus and task factors on Achilles tendon reflexes evoked early during a preparatory period

Effects of Stimulus and Task Factors on Achilles Tendon Reflexes Evoked Early During a Preparatory Period

Received 25 August 1981

SCHEIRS, J. G. M. AND C. H. M. BRUNIA. *Effects of stimulus and task factors on Achilles tendon reflexes evoked early during a preparatory period.* PHYSIOL. BEHAV. 28(4)681–685, 1982.—The effects of intensity, duration and modality of a warning signal on tendon (T) reflexes evoked during the initial phase of a preparatory period of 4 sec were investigated. Reflexes were evoked simultaneously in both legs, from 0 to 350 msec after warning signal onset in steps of 50 msec. The required response was a plantar flexion of the right foot. A facilitation of reflexes was seen within 150 msec after warning signal onset, showing a somewhat longer latency for visual as compared to auditory signals. An effect of intensity was found in the auditory modality only, where the louder of two warning signals yielded a clear peak at 100 msec while the softer stimulus caused no significant departure of Achilles tendon reflexes from baseline. The time course of facilitation in the auditory modality was influenced by warning signal duration as well, although this effect was only marginally significant. There were no effects of physical warning signal parameters on reaction time. A comparison with an experiment in which non-signal stimuli were presented alone, pointed to aspects of the preparatory process which were manifest at the spinal level as early as 200 msec after warning signal onset.

Achilles tendon reflex Motor preparation Reaction time Reflex facilitation

IT IS well known that the presentation of an auditory stimulus can have facilitating effects on monosynaptic spinal reflexes in man. The amplitude of the quadriceps stretch reflex, for instance, is increased when auditory stimuli of different intensities are presented prior to and during reflex evocation. The higher intensities of the tone result in a greater increase [10], while maximal facilitation is found at about 100 msec after tone onset [1]. The electrically evoked Hoffmann (H) reflex proves to be sensitive to this audio-spinal facilitation as well [16].

The H reflex and the Achilles tendon (T) reflex can be evoked during the foreperiod of a warned reaction time experiment. Changes in reflex amplitudes during the foreperiod are an index of changes in excitability of alpha motoneurons innervating the triceps surae muscle, and in presynaptic inhibition acting on the group Ia fibres. When the required response is a plantar flexion of one of the feet, a movement for which the same muscle has to be activated voluntarily, these changes in reflex amplitudes can be thought to reflect elements of the preparatory process taking place in the subject in anticipation of the response. Previous experiments employing such an experimental paradigm showed that an initial increase in H reflex amplitudes could be found at about 100 or 200 msec following the warning signal, both when short (1 sec) as well as long (4 sec) foreperiod durations were used [6,15]. It has become clear recently [7], that an early peak is also present when T reflexes are evoked during a 4 sec foreperiod.

The blink reflex is also used as a test for motorpreparation in humans [4]. The first component of this reflex was shown to be enhanced by preliminary stimulation in a comparable fashion [18].

It has been argued that this early facilitation might be related to the presentation of the warning signal, and that it is independent of the kind of response, i.e., a foot or finger movement [6]. The question then arises whether the increase is triggered by the alerting properties of the warning signal per se, or by the signal value that has been attributed to it as well. In other words: is the early peak determined by physical parameters of the warning signal, by aspects of the preparatory process, or by both?

There is some evidence that preparatory processes do play a role at the beginning of the foreperiod. It was found about a decade ago that the amount of T reflex facilitation observed during the first sec after onset of a tone, depended on whether a response was required to tone offset 4 sec later [9]. In addition, data from our laboratory (Haagh, communication at the 22nd. Tagung experimentell arbeitender Psychologen, Tübingen, 1980) indicate that the early peak is larger when the probability that the reaction signal is going to be presented is less than one. Finally, the amplitude and the latency of the early peak have been shown to depend on the length of the foreperiod that is employed, at least when these foreperiods are of a very short duration [19].

The present experiment was aimed at the question of whether or not the early facilitation of T reflex amplitudes in

a 4 sec foreperiod would be influenced by the signal value of the warning signal, and whether or not non-task factors such as intensity, duration and modality would play a role as well.

METHOD

Subjects

Eighty right-handed subjects, 42 males and 38 females, took part in the experiments. Their age varied between 16 and 39 years (mean age: 22.4 years). The subjects, the majority of them being college students, were paid for their cooperation.

Apparatus

Subjects were seated comfortably in a specially designed chair, placed in a dimly illuminated, soundproof and electrically shielded room, with their feet strapped to a footplate. The knees were positioned in approximately 120° of flexion while the ankle was set at 90°. T reflexes were evoked in both legs simultaneously by means of two Brüel and Kjaer 4809 vibration exciters, which were directed at a right angle to the Achilles tendon at the level of the lateral malleolus. The vibration exciters were triggered by a 9 msec pulse of variable amplitude, produced by two Brüel and Kjaer 2706 power amplifiers.

Either an auditory or a visual stimulus served as the warning signal (WS). The auditory stimulus was produced by a Sonalert (2800 Hz) centered behind the subject. Its duration was 100 or 200 msec, while its intensity was either 65 or 85 dB (A) at the level of the subject's ears. Three different combinations of duration and intensity were made. These combinations were employed pairwise as follows: the 100 msec–85 dB and the 200 msec–85 dB tones, which shall hereafter be referred to as the short and long stimulus respectively, and the 100 msec–65 dB and the 100 msec–85 dB tones, which will be called the soft and loud stimuli. A red LED-display (surface area: 9 cm^2) placed at eye-level about 2 m in front of the subject was used as the visual WS. The duration of this visual WS was 100 msec; its intensity was 15 or 200 cd/m^2 against a 3 cd/m^2 background luminance (as measured by a Minolta auto spot-1 luminance meter). The two visual warning signals will be referred to as the weak and intense visual stimuli, respectively.

A second LED-display (green, 9 cm^2, 20 cd/m^2), positioned next to the red one, served as the reaction signal (RS) throughout the experiments. The RS lasted for 50 msec. A square wave tone (500 Hz, duration: 1 sec, intensity: 85 dB) was used as a feedback signal (see procedure).

Experimental procedures as well as reaction time (RT) data acquisiton were accomplished by means of a DEC Lab 8/e computer.

The electromyographic responses were recorded via two Ag-AgCl surface electrodes attached 4 cm apart on the distal part of each soleus muscle. The signals were amplified by Hellige EE preamplifiers (−3 dB bandwidth: 5.3–1000 Hz) and recorded on magnetic tape (Hewlett-Packard 3960; bandwidth 0–312 Hz). A DEC PDP 11/10 computer was used for analog to digital conversion (sample frequency: 2048 Hz) as well as measurement of the peak to peak amplitudes of the reflexes.

Procedure und Data Analysis

The experiment consisted of four conditions. Twenty subjects participated in each of these four conditions. In condition I (passive listening) a non-signal stimulus was presented alone without a response requirement. The interval between two successive signals was 20 sec. In conditions II, III and IV (the reaction time tasks) a WS was presented, followed 4 sec later by the RS. Subjects were instructed to respond as quickly as possible to the RS by making a plantar flexion with their right foot and thereby closing a microswitch mounted under the footplate. In conditions II, III and IV, each foreperiod of 4 sec was followed by an intertrial interval of 16 sec.

In all four conditions, one out of two possible warning stimuli (i.e., non-signal stimuli in condition I) was chosen pseudo-randomly, each stimulus being presented on 50% of the total number of trials. The stimuli used in conditions I and II were the soft and the loud one. Thus, the effect of WS intensity and the effect of the task factor (passive listening vs. preparation for a response) could be investigated. In condition III, the short and long stimuli were used in order to study possible effects of the duration of an auditory WS. In condition IV, the weak and intense stimuli were employed in order to compare WS intensity effects in different modalities.

Reflexes were evoked in a pseudo-random order, 8 times at each of 8 different temporal measuring points and for each of the two warning stimuli: at 0, 50, 100, 150, 200, 250, 300 and 350 msec after WS onset. Only one reflex was evoked on each trial. An experimental session for a particular subject consisted of 128 trials. After each trial, a control reflex was evoked pseudo-randomly at 6, 8 or 10 sec after the RS (i.e., at 10, 12 or 14 sec after the non-signal stimulus in condition I).

The feedback signal was presented to the subject whenever a response occurred before RS presentation on a certain trial in condition II, III or IV, or when no response had been given at all within 450 msec after the RS. All subjects were given some practice trials prior to the experiment, and were instructed not to make gross movements during the session. An extra financial reward was promised in case of very fast and errorless responding.

After completion of the experiment, peak to peak amplitudes of the T reflexes were measured. Individual control levels were obtained for each leg and each type of WS by averaging the corresponding control reflexes. Mean reflex amplitudes of each of the 8 different measuring points were calculated per subject and expressed as percentages of the individual control levels. The individual percentage scores were used for statistical analysis, the overall averaged scores for the illustrations.

In order to prevent the data from being contaminated by premature or late responses, trials with RTs shorter than 100 msec or longer than 450 msec were excluded from the analysis. This procedure did not result in less than 5 remaining observations per measuring point for each WS in any subject.

RESULTS

Conditions I and II

Mean T reflex results from conditions I and II, where the soft and loud warning signals were employed, are depicted in Fig. 1. The data were analysed in a S(A)×B×C×D ANOVA, the factors being the between-subjects variable Condition (i.e., reaction time task vs. passive listening) and the within-subjects variables Intensity Level (soft vs. loud), Registration Side (left vs. right leg) and Temporal Measuring Points

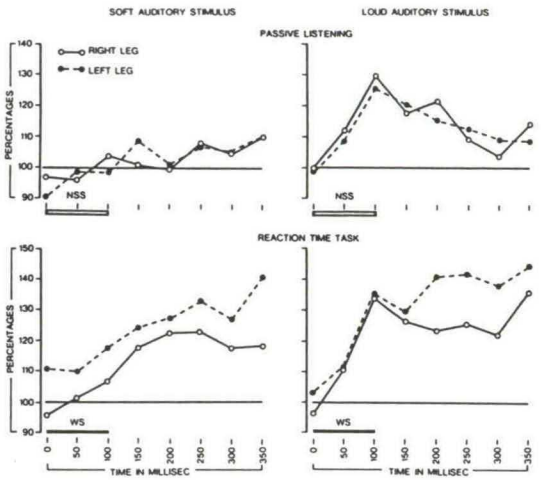

FIG. 1. Mean T reflex amplitudes during the early phase of a 4 sec foreperiod, expressed as percentages of the baseline level. Condition I (passive listening) is at the top, condition II (reaction time task) is below. The required response in the reaction time task was a plantar flexion of the right foot. Trials in which the soft (65 dB) auditory stimulus was presented are at the left, trials in which the loud (85 dB) one was used are at the right. Time is in milliseconds after onset of the non-signal stimulus (NSS) or the warning stimulus (WS).

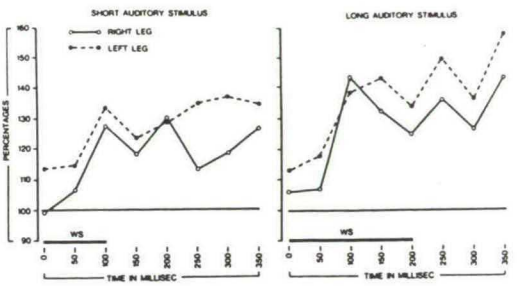

FIG. 2. Mean T reflex amplitudes in condition III. The short auditory stimulus (100 msec) is at the left, the long one (200 msec) at the right. The required response was a plantar flexion of the right foot.

(from 0 up to 350 msec after WS onset, in steps of 50 msec). Only significant ANOVA results are reported.

There are main effects of Condition, $F(1,38)=14.71$, $p<0.01$, of Intensity Level, $F(1,38)=21.84$, $p<0.01$, and of Temporal Measuring Points, $F(7,266)=10.50$, $p<0.01$. The time course of reflexes is different for the two types of WS (Intensity Level×Temporal Measuring Points interaction effect: $F(7,266)=4.56$, $p<0.01$). When the loud stimulus is used, there is a clear peak at 100 msec, while a more gradual time course can be observed following the soft stimulus, both in the reaction time and the passive condition.

There are significant interaction effects of Condition×Registration Side, $F(1,38)=4.02$, $p<0.05$, and of Condition×Temporal Measuring Points, $F(7,266)=2.50$, $p<0.05$. Thus, the differences between legs and the time course of reflexes are both dependent on the task factor. As can be seen from Fig. 1, and especially from the loud stimulus data, the differences between the reaction time and the passive condition are most pronounced during the second part of the recording period (from 200 up to 350 msec). Reflexes during this second part of the recording period remain elevated in the reaction time condition, while they tend to decrease or remain at about baseline level in the passive condition. Scheffé posthoc tests done on the first 4 and the last 4 measuring points, respectively, reveal that the Condition main effect is due, indeed, to the values observed during the second part of the recording period (value of contrast for last 4 measuring points: 0.86, Scheffé critical s: 0.44, $p<0.01$).

Student t-tests were carried out on the data to see whether reflexes during the foreperiod differed from the baseline (100%) level. In condition I, reflexes following the soft stimulus do not differ from baseline, except in the left leg at 0 and 250 msec ($t=-4.79$, $df=19$, $p<0.01$ and $t=2.10$, $df=19$, $p<0.05$). Reflexes following the loud stimulus show a significant difference in both legs from 50 up to 250 msec ($t>2.09$, $df=19$, $p<0.05$). In condition II, measuring points from 50 msec up to 350 msec differ from baseline in both legs and for both types of WS, except in the right leg following the soft stimulus at 0, 50 and 100 msec ($t>2.19$, $df=19$, $p<0.05$).

Condition III

Figure 2 displays the results of condition III, where the short and long warning signals were used. An S×A×B×C ANOVA was carried out on the data, the factors being Duration, Registration Side and Temporal Measuring Points. A main effect of the factor Temporal Measuring Points is present, $F(7,133)=6.67$, $p<0.01$, while the factor Duration just fails to reach the criterion level, $F(1,19)=3.93$, $0.05<p<0.06$.

Reflex amplitudes after the short stimulus differ significantly from baseline at all measuring points in the left leg, and at 100, 150 and 200 msec in the right leg ($t>2.20$, $df=19$, $p<0.05$). When the long stimulus is considered, amplitudes in the non-involved (left) leg differ from baseline from 50 msec onwards and in the involved (right) leg from 100 msec onwards ($t>2.12$, $df=19$, $p<0.05$).

Condition IV

The results of condition IV are presented in Fig. 3. An S×A×B×C ANOVA was performed on the data, the factors being Intensity Level, Registration Side and Temporal Measuring Points. The factor Temporal Measuring Points proves to be significant, $F(7,133)=11.88$, $p<0.01$. There is also a significant interaction effect of Registration Side×Temporal Measuring Points, $F(7,133)=2.50$, $p<0.05$. No Intensity Level main effect is observable in this condition.

Differences between reflex amplitudes and baseline levels are significant from 100 up to 350 msec in the left leg and

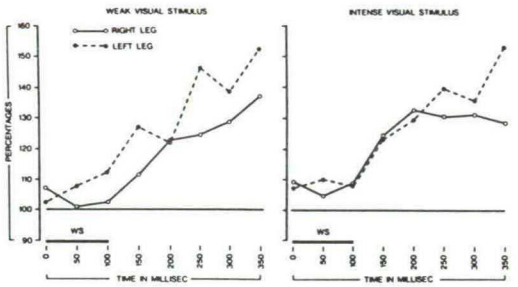

FIG. 3. Mean T reflex amplitudes in condition IV. The weak visual stimulus (15 cd/m²) is at the left, the intense one (200 cd/m²) at the right. The required response was a plantar flexion of the right foot.

from 150 up to 350 msec in the right leg, when the weak stimulus was presented ($t>2.18$, $df=19$, $p<0.05$); significant differences after presentation of the intense stimulus are found from 50 msec onwards and from 100 msec onwards, respectively ($t>2.30$, $df=19$, $p<0.05$).

Baseline Levels and Reaction Times

Control reflex amplitudes in the right and left leg, constituting baseline levels, do not differ significantly in any of the four conditions ($t<1.08$, $df=19$, in all conditions). So it seems legitimate to compare reflexes evoked during the foreperiod in the two legs.

RTs were calculated per subject after removal of the erroneous responses as described earlier, and averaged over subjects in each condition. These grand means are graphically presented in Fig. 4. According to a two-way ANOVA, there are no significant differences in RTs between or within conditions. Standard errors of the mean RTs and mean percentages of correct responses are given in Fig. 4 as well.

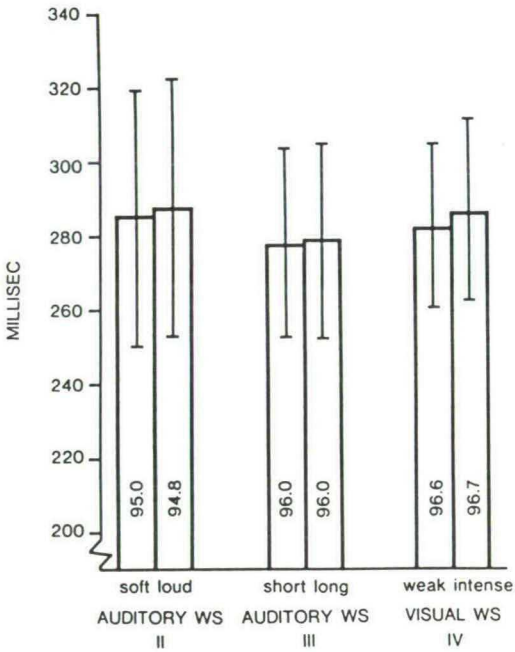

FIG. 4. Mean reaction times over correct responses for conditions II–IV. Standard errors of the mean are indicated by vertical lines. Percentages of correct responses are given in the bars.

DISCUSSION

The louder of two auditory non-signal stimuli has a clear facilitating effect upon T reflex amplitudes observed up to 250 msec after stimulus onset, while no significant increase is present following the softer stimulus. These results are compatible with the findings of Davis and Beaton [10]. Facilitation reaches a peak at 100 msec for the loud stimulus. Beale [1] examined the knee-jerk and found a first peak at a similar latency. He ascribed this peak to the influence of descending neural activity on the alpha motoneurons in the spinal cord, as the latency of 100 msec would, in his opinion, not allow afferent activity due to activation of the gamma system to play a role. Apart from such an argument, there is ample evidence showing that reflex potentiation in general occurs independently of the fusimotor system [20]. In addition, it appears that during preparation for a movement there is no activation of fusimotor neurons at all, at least when there is no concomitant EMG activity in the involved muscle [8]. This points to either the mechanism of alpha-gamma coactivation, or the influence of a central process on the alpha motoneurons alone as a modulator of reflex gain.

When the stimulus is given signal value and comes to serve as a WS in a RT experiment, results comparable to the passive condition are obtained during the first 150 msec after WS onset. This finding contrasts with the results of Semjen, Bonnet and Requin [19], who found differential effects of a click on H reflex amplitudes, dependent on whether the click was presented alone or served a warning function. But here, foreperiod duration, which was only 300 msec in the latter study, is probably a confounding factor.

From 200 msec onwards, reflexes are found to be larger than during the same period in the passive condition, thus revealing the contribution of a task factor to reflex enhancement as early as a few hundred milliseconds after the beginning of the foreperiod. This finding is compatible with the results of Bonnet [5], as far as the initial facilitation was found to be task dependent. His assertion, however, that these initial effects, up to 300 msec after the WS at least, "are probably not connected with motor processes of preparation in the strict sense" needs further exploration. A clear distinction between what are called attentional processes on the one hand, and motor preparation on the other hand, can not easily be made on the basis of these experiments.

Our results suggest the presence of a general arousal process triggered by the WS, to which after a few hundred milliseconds the impact of a task related process is added. The fact that from 150 msec onwards after the loud WS in condition II, reflex amplitudes are smaller in the involved than in the non-involved leg gives more credence to this suggestion. In a former study [7], it was found that during a 4 sec foreperiod, reflex amplitudes in the leg involved in the

response were smaller than in the non-involved leg. This was interpreted as a first index of specificity in the preparatory process, because it was found in the left leg preceding a left sided response and in the right leg preceding a right sided response. Since in the present experiment only right sided responses were studied, we are inclined to interpret the consistently smaller amplitudes in the right leg in a similar way, although statistical significance is reached only in condition II.

The results of condition III show that the time course of T reflexes may also be influenced by the duration of an auditory WS, although the observed effect is small and not highly significant. It is conceivable that rate of change of a warning signal is a more important characteristic in determining the amount of reflex facilitation than total energy in the stimulus, as was proposed by Graham [12] with regard to the human startle response.

In condition IV, no effect of stimulus intensity is found in the visual modality. Perhaps the chosen intensities were, although clearly discriminable, too proximate to produce any effect. An important result of this experiment is the gradual increase of reflexes which is observed after both visual warning stimuli. We would like to suggest that this different time course is due to the delayed onset of the facilitation that is present here, as compared with the immediate rise seen after the auditory warning signals. The general arousal triggered by the WS and the preparatory process, both giving rise to a reflex increment, can be thought to coincide during the later part of the recording period. The delay in the visual modality is consistent with the notion of an "immediate arousing effect" of auditory stimuli, stemming from reaction time research [3]. This modality effect is probably not restricted to changes at the spinal level, as a widespread increase in excitability of cortical neurons in both sensory and motor systems has been found after presentation of a non-habituated stimulus in the cat, showing a longer delay for visual stimuli of about 30 msec [17]. An alternative hypothesis is that it is not the modality effect which is of major importance in determining the difference in slope between the curves of conditions I, II, or III and of condition IV, but that it is simply a matter of stimulus intensity, which could have been at the lower end of the scale for both the weak and the 'intense' visual warning. The high degree of similarity between the curve following the soft auditory WS (Fig. 1) and both curves following the visual WS (Fig. 3) makes this explanation plausible.

Physical WS-parameters have no effect on RT in our experiments. This corroborates the results of Gaillard [11], who in a CNV study employing a 3 sec foreperiod, found no effect of WS modality on RT. On the other hand, Loveless and Sanford [14] did find an effect of WS intensity (auditory) on RT, but in their study, the WS was continuously presented during the foreperiod. In other studies, both negative [2] as well as positive [13] correlations between WS intensity and RT were reported for short as well as long foreperiod durations. It should be noticed, however, that in all four conditions of the present experiment, the reflex-eliciting stimulus applied during the foreperiod could have had the unwanted effect of serving as an extra warning, thereby possibly obscuring the differential effect on RT, due to the WS itself.

Taken together, our results support the view that the process of preparation as measured by T reflexes in a RT task is manifest early during the foreperiod; it seems to go along with or follow shortly after the effects due to the alerting properties of the warning signal per se.

ACKNOWLEDGEMENTS

This research was supported by the Dutch Organization for the Advancement of Basic Research ZWO (grant 78–384).

We would like to thank Martijn Berger for the use of his ANOVA-program, Stephan Haagh for his helpful comments and Jan Pijnenburg for preparing the illustrations.

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Appendix 3.

Achilles tendon reflexes and surface EMG activity during anticipation of a significant event and preparation for a voluntary movement

Achilles Tendon Reflexes and Surface EMG Activity during Anticipation of a Significant Event and Preparation for a Voluntary Movement[1]

ABSTRACT. Achilles tendon reflexes were evoked bilaterally during and shortly after an interstimulus-interval (ISI) of 4 s and expressed as percentages of an averaged control reflex. Surface EMG of the soleus muscles was recorded continuously during the ISI, and expressed as percentages of a control EMG level. Three types of tasks were introduced, according to a between subjects design. Condition I consisted of a guessing task, involving anticipation of the second stimulus (S2) and not requiring a motor response. Conditions II and III were a warned choice and simple RT task respectively, the motor response to S2 being a plantar flexion of either the left or right foot in Condition II, and a plantar flexion of the right foot in Condition III. The results can be stated as follows:

1. **Anticipation of a stimulus is not sufficient for a reflex increase to occur during an ISI. Preparation for a movement seems to be a necessary condition.**
2. **The reflex increase during preparation is rather independent of the amount of selectivity in the preparatory process; simple and choice RT tasks yield similar results, although the mean RTs do differ.**
3. **A difference between the involved and non-involved legs in the simple RT task is not found in the present experiment, as opposed to other studies. The particular instruction given to the subjects could be of importance in producing this difference.**
4. **Reflex changes cannot simply be accounted for by changes in background EMG of the agonist, as the EMG time course shows no changes over time in either condition.**

EVOKING MONOSYNAPTIC SPINAL REFLEXES during the foreperiod of a warned reaction time (RT) task has become a standard technique in

This research was supported by the Dutch Organization for the Advancement of Basic Research Z. W. O. (grant 78-384). The authors wish to thank Ton Aalbers for his work in designing part of the amplification equipment and Jan Pijnenburg for drawing the figures. Thanks are also due to two anonymous reviewers for their valuable comments.

the study of the human motor-system during preparation for a voluntary movement.

In the case of Achilles tendon (T) reflexes evoked prior to an extension movement of one of the feet, an increase of reflex amplitudes recorded in the soleus muscle uninvolved in the execution of the response has been reported by several investigators (Requin, 1969; Requin & Paillard, 1971; Brunia, Scheirs, & Haagh, 1982). In these studies, a relative depression of reflexes evoked in the involved soleus muscle was observed, although some controversy seems to exist concerning the depth of this depression (Brunia, 1983). When the electrically evoked Hoffmann reflex is employed, equivocal results indicating either the presence or the absence of a difference between involved and uninvolved soleus muscles have been reported (Semjen, Bonnet, & Requin, 1973; Requin, Bonnet, & Semjen, 1977; Brunia & Vuister, 1979).

It was suggested (Requin & Paillard, 1971; Brunia et al., 1982) that during preparation two distinct processes would contribute to the T reflex results as described above: first, a general activation influencing both the involved and non-involved motoneuron pools and second, a selective inhibitory process confined to the spinal motor structures which are involved in the response execution. These two processes then would, by summation, cause the reflexes evoked in the involved leg to show only a minor or no departure from baseline.

In the present experiment, we will elaborate on the T reflex time course during a four second foreperiod as was described by Brunia et al. (1982). Our aim is to investigate whether a reflex increase is dependent on a motor response to be performed after the foreperiod. It could well be that stimulus anticipation leads to similar results and that a motor task is not a prerequisite. A second purpose of the experiment concerns the nature of the difference between reflex changes in the involved and non-involved legs. If this difference reflects the selective aspects of the preparatory process, as was proposed, then reducing the amount of selectivity by introducing a choice instead of a simple RT task would probably weaken or eliminate this difference.

Finally, monitoring the surface EMG of both involved and non-involved soleus muscles is considered to be of importance in this experiment, as background EMG levels of involved muscles were found to be elevated during the foreperiod of some RT experiments (Requin, 1965; Brunia & Vingerhoets, 1980; Haagh & Brunia, 1984), while the level of tonic activation in the agonist muscle may influence the gain of the tendon reflex loop (Ott & Gassel, 1969). Since reflex amplitudes are supposed to reflect subliminal changes in motoneuron excitability, the presence of background EMG activity may seriously limit the interpretability of the reflex results.

Methods

Subjects

Sixty right-handed subjects, 32 females and 28 males, took part in the experiments. They ranged in age from 17–39 years (mean = 21.1 years).

Most of the subjects were recruited from the undergraduate psychology course and were paid for their participation.

Apparatus

The subjects were seated comfortably in a specially designed chair placed in a dimly illuminated, soundproof, and electrically shielded cubicle with their feet strapped to movable footplates. Microswitches were placed under these footplates for the recording of RTs. The knees were positioned in approximately 120° of flexion, while the ankle was set at 90°.

Submaximal T reflexes were evoked by means of two Brüel and Kjaer 4809 vibration exciters that were directed at a right angle to the Achilles tendon at the level of the medial malleolus. The vibration exciters were triggered by a 9 ms pulse of constant amplitude produced by two Brüel and Kjaer 2706 power amplifiers.

An auditory stimulus (2800 Hz, 100 ms, 85 dB[A]) delivered by means of a loudspeaker centered behind the subject served as S1. Two circular red LED displays (surface area: 9 cm^2) were positioned side by side about 2 m in front of the subject. S2 consisted of the illumination of one of these displays (50 ms, 200 cd/m^2). A 500 Hz 80 dB(A) tone presented during 1 s was used as a feedback signal (see procedure).

The electromyographic responses were recorded via two Ag-AgCl surface electrodes attached 5 cm apart on the distal part of each soleus muscle. The signals were amplified by two differential amplifiers (−3 dB bandwidth: 3.8–520 Hz) that were adapted in our laboratory to allow for recording of both the low level background EMG and the reflex potentials, which are of much larger amplitude, on the same channel of a magnetic tape. A Hewlett and Packard 3960 instrumentation recorder (flat frequency response within ±1 dB: 0–312 Hz) was employed for storage of these signals.

Experimental procedures were controlled by a DEC Lab 8/e computer. A DEC PDP 11/10 computer was used for analog to digital conversion of the data, measurement of the peak-to-peak amplitudes of the reflexes, and integration of the EMG. Final calculations were done on a DEC VAX 11/780 computer.

Procedure

The experiment consisted of three conditions in a between subjects design, twenty subjects taking part in each condition. Each condition consisted of 104 trials. In each trial, presentation of S1 was followed 4 s later by presentation of S2. This interstimulus-interval (ISI) was followed by an intertrial-interval (ITI) of 18 s. Reflexes were evoked in a pseudo-random order, 8 times at each of 13 points in time: at 0, 100, 200, 500, 1000, 2000, 3000, 3500, 3700, 3900, 4000, 4100 or 4150 ms after S1 onset. Only one reflex was evoked during each ISI or shortly afterwards.

A control reflex was evoked at 6, 8 or 10 s after S2 in each trial. Reflexes were always evoked simultaneously in both legs. Prior to the experiment, the power amplifiers were adjusted to obtain reflexes of about the same amplitude in the left and right leg.

Background EMG of the soleus muscles was recorded continuously. RTs were measured to the nearest ms and subsequently printed on paper.

In Condition I ("guess"), subjects were instructed to predict whether S2 would be presented on the left or right side by pressing a key with the corresponding index finger (cf. Donchin, Gerbrandt, Leifer, & Tucker, 1972). Predictions (i.e., key-presses) had to be made during the later part of the ITI, amply after the evocation of the control reflex and more than 1 s before presentation of S1. No motor response other than the key-press was required in this condition. Either the left or the right light was presented as S2, each stimulus occurring in 50% of the total number of trials. Presentation order varied pseudorandomly, in such a way that the lights occurred no more than two times at the same side successively. By paying attention to S2, subjects were able to make correct predictions in about 70% of the trials. They received an extra financial reward according to the number of correct guesses.

In Condition II ("choice RT"), subjects were instructed to respond as quickly as possible to S2 by making a plantar flexion with either their left or right foot, depending on whether S2 would be presented on the left or right side. Stimulus configuration was the same as in Condition I. Errors, that is, premature (RT $<$ 100 ms) or late (RT $>$ 500 ms) reactions as well as wrong leg responses were followed immediately by auditory feedback.

In Condition III ("simple RT"), the response requirement was a plantar flexion of the right foot irrespective of whether the left or right light was presented. RTs $<$ 100 ms or $>$ 450 ms were considered errors and were followed by the feedback stimulus. In Conditions II and III a low error rate was rewarded financially.

Prior to all conditions, subjects were given about thirty practice trials and were instructed to relax and not to make gross movements during the session.

Data Analysis

EMG and reflex responses obtained in the experiments were digitized off-line (sample frequency: 1024 Hz). Trials containing errors were discarded from further analysis. Peak-to-peak amplitudes of reflexes were measured and means were calculated at each of the points in time for each subject. Mean amplitudes during the ISI were expressed as percentages of the mean control reflex amplitude for each leg separately. The EMG was rectified and integrated over successive 100 ms epochs during the ISI and expressed as percentages of the mean rectified EMG calculated over the sixth second of each ITI. In every trial, a period of 500 ms in the EMG immediately following the moment of reflex evocation was not analysed to prevent the resting EMG-level from being contaminated by the reflex contraction or its electromechanical aftereffects.

Individual EMG percentage scores averaged over 5 successive epochs as well as individual T reflex data were used for statistical analyses. Eventually, EMG as well as T reflex data were averaged over subjects for illustrative purposes.

Results

Physiological measures

Averaged T reflex amplitudes during and shortly after the ISI as well as the corresponding surface EMG from all three conditions are shown in Figures 1, 2, and 3. Insets show data from separate trials in which subjects guessed "left" and "right" (Figure 1) or responded to stimuli located at the left and right side (Figures 2 and 3), respectively.

Considering the reflex data (grand averages) first, it appears from Figure 1 that during anticipation of S2, reflexes remained at the baseline level; except from an early peak at 100–500 ms and a second increase immediately following S2 at 4100 and 4150 ms. *T* tests on means (two-tailed) showed that reflexes elicited at these points in time differed significantly from baseline in both the left and the right leg ($t \geq 2.29$, $df = 19$, $p < .05$). During the choice RT task (Figure 2), reflexes were increased at all points in time except at 0 ms in both the left and the right leg and at 2000 ms in the left leg ($t \geq 2.23$, $df = 19$, $p < .05$). Reflexes in the simple RT task were above baseline at all points in time except at 0 ms (Figure 3, $t \geq 2.77$, $df = 19$, $p < .05$).

With respect to the EMG, *t* tests on means indicated that there were no significant deviations from baseline in any condition. In general, the observed changes in background EMG were very small (20% deviations from baseline maximally in all but three of the subjects), whereas the decreased EMG level during the choice RT task (Figure 2) was largely due to one individual. The absolute baseline EMG amplitudes averaged at values smaller than 1.5 μV in all subjects.

To test whether there were any differences between the left and right legs or differences in time course, three analyses of variance (ANOVAs) were carried out on the complete data set. For reasons of interpretability, the reflex data obtained during the ISI (0-4000 ms) and those recorded afterwards (4000-4150 ms) were analyzed separately, while the EMG data obtained during the ISI were analyzed in the third ANOVA. The factors in all three analyses were the between-subjects variable Condition, and the within-subjects variables Recording Side (levels: left and right) and Points in Time (levels: measuring points 1–11 and 11–13 in the reflex analyses and 1–8 [500 ms epochs] in the EMG analysis). The results of the three ANOVAs are summarized in Table 1.

Considering the reflex data during the ISI first, it appears that relative amplitudes were different for the three conditions. A Scheffé a posteriori test revealed that it was the difference between the "guess" condition and either of the other two conditions that caused this effect (value of contrasts: 17.95 and 19.40 respectively, critical s: 15.51, $p < .01$). Furthermore, it can be seen from Table 1 that the reflex time course showed

Table 1
Results of ANOVAs on T reflexes and surface EMG of the soleus muscles.

	T Reflexes				EMG	
	0–4000 ms		4000–4150 ms		0–4000 ms	
Source	*df*	*F*	*df*	*F*	*df*	*F*
Condition (A)	2/57	9.71*	2/57	16.07*	2/57	1.03
Recording Side (B)	1/57	0.16	1/57	8.00*	1/57	0.01
Points in Time (C)	10/570	10.14*	2/114	46.40*	7/399	1.00
A x B	2/57	1.68	2/57	3.21*	2/57	0.93
A x C	20/570	3.87*	4/114	7.89*	14/399	2.18*
B x C	10/570	0.82	2/114	12.98*	7/399	1.47
A x B x C	20/570	1.10	4/114	6.72*	14/399	0.44

* significant effects ($p < .05$)

significant changes during the ISI, these changes being dependent on which condition was considered. Significant left-right differences could not be detected.

The significant main effects of the second ANOVA indicated that, after the ISI, reflexes were different for the three conditions and for the left and right soleus muscle as well as for the three points in time. Since all possible interactions with these factors were significant, additional a posteriori testing according to Scheffé's method was done. This testing revealed that a significant difference between the left and right soleus muscle after S2 was only present in the simple RT task (value of contrast in Condition III: 51.35, critical s: 43.61, $p < .05$). The increase seen after S2 was smaller in the "guess" condition than in the other two conditions (contrast: 75.67, s: 42.23, $p < .01$).

With regard to the EMG data, the ANOVA yielded only one significant result, which points to a different time course, depending on which experimental condition was employed (see Table 1).

Finally, ANOVAs were performed on the split data sets as shown in the figure insets. During the ISI no significant left-right differences were obtained in any condition. Thus, the fact that subjects were able to predict the location of S2 in more than 50% of the trials did not contribute to the averaged results.

When testing the left-right differences in control values of T reflexes and EMG by means of *t* tests, significance was not reached in any condition. This result allows for reliable comparison of reflex changes in the left and the right leg.

Behavioral measures

The mean proportion of correct predictions in Condition I was .65 (total range: .50–.73).

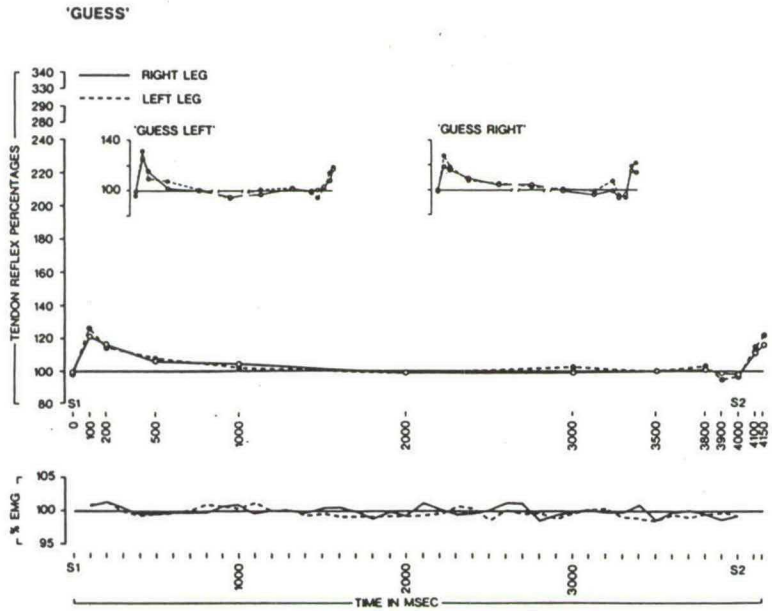

Fig. 1—Averaged T reflex amplitudes and surface EMG during an interstimulus-interval of 4 sec (Condition I, "guess"). Reflexes and EMG are expressed as percentages. The averaged control value = 100%. The subject's task was, prior to S1, to make a prediction about the occurrence of S2 on the left or on the right side. Insets show trials with the subjects guessing "left" and "right" respectively.

Fig. 2—Averaged T reflex amplitudes and surface EMG during an interstimulus-interval of 4 sec (Condition II, "choice RT"). Reflexes and EMG are expressed as percentages. The averaged control value = 100%. The subject's task was to make a plantar flexion with either the left or right foot, depending on whether S2 occurred on the left or on the right side of the stimulus display. Insets show trials with the subjects responding with their left and right foot respectively.

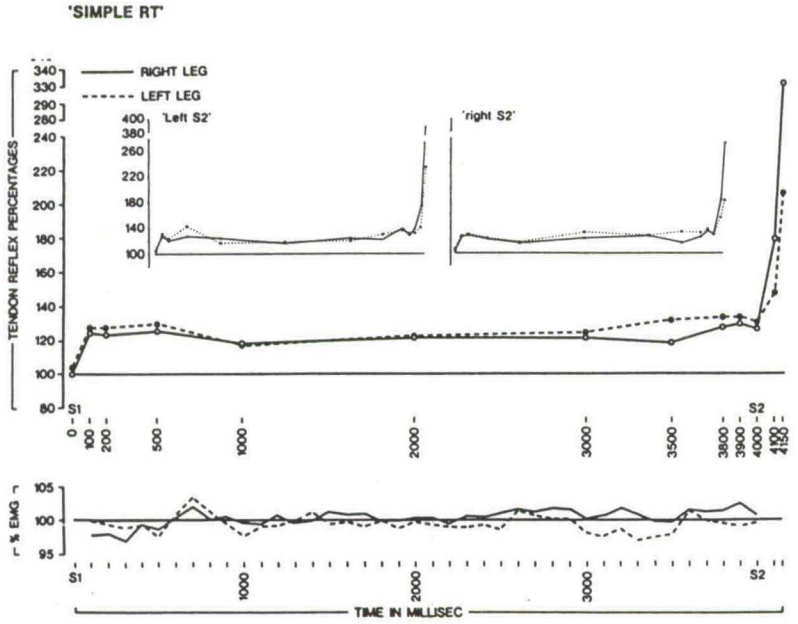

Fig. 3—Averaged T reflex amplitudes and surface EMG during an interstimulus-interval of 4 sec (Condition III, "simple RT"). Reflexes and EMG are expressed as percentages. The averaged control value = 100%. The subject's task was to make a plantar flexion with the right foot, irrespective of whether S2 occurred on the left or on the right side of the stimulus display. Insets show trials with S2 occurring on the left and right side respectively.

The mean RTs and corresponding standard deviations from Conditions II and III are given in Figure 4. The difference between the averaged response times from the choice and simple RT tasks was significant ($t = 4.30$, $df = 19$, $p < .01$). No significant differences were found within conditions when trials with S2 presentation on the left side were compared with trials in which S2 was presented on the right side.

Error rates are illustrated also in Figure 4. The mean percentage of errors made in the simple RT task was somewhat larger than in the choice RT task, while in the choice RT task left-sided responses caused more errors than right-sided responses. Neither of these differences, however, reached significance. The majority of the errors consisted of late responses (62% in the choice RT task and 90% in the simple RT task) and wrong leg responses (36% in the choice RT task). Premature reactions were few (2% in the choice RT task and 10% in the simple RT task).

Discussion

The main point of this experiment was to test the assumption that not only motor preparation but also stimulus anticipation would give rise to a T reflex increment. The results showed that the assumption does not hold. The only effects in the stimulus anticipation condition were two distinct peaks immediately following S1 and S2. The first peak can be as-

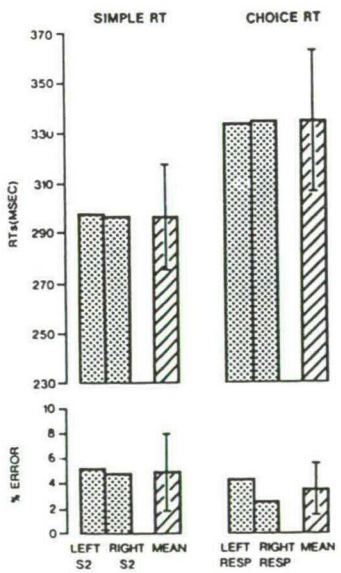

Fig. 4—Mean reaction times and error rates in Condition II ("choice RT") and Condition III ("simple RT"). Standard deviations are indicated by vertical lines.

cribed to the physical properties of the auditory S1 as it was found in an earlier experiment when a similar stimulus was presented without a task requirement (Scheirs & Brunia, 1982). Whether the second peak is determined solely by physical properties of the second stimulus is not clear, as performing the guessing task involves cognitive processing of S2 as well. However, this peak indicates that the subjects acted according to instructions and did not involve in the task without actually watching S2.

Preparation for a movement thus appears to be a necessary condition for a T reflex increase to occur during an ISI. It should be kept in mind, however, that we only used one type of (non-motor) task to test this assumption, and there is no easy way to decide whether the mental load imposed on the subject is of equal magnitude prior to both the motor and non-motor tasks.

In contrast, reflexes were found to be increased during the entire foreperiod of the simple and choice RT tasks. The time courses were more or less the same in both RT paradigms, with no significant differences present between the left and right leg in either condition. In case of the choice RT task, this is easy to reconcile with the nature of the task itself, which calls for no selectivity in the preparatory process. In line with this finding, are the behavioral data that showed no significant left-right differences in RTs or error rates.

However, the difference between the involved and non-involved legs in the simple RT task, which was a stable finding in former experiments employing both foreperiods of one and four seconds duration (Requin, 1969; Requin & Paillard, 1971; Brunia et al., 1982; Brunia, 1983), could not be replicated. When comparing the simple RT condition of our present experiment with the similar condition of the Brunia et al. (1982) study, there are two main differences which could reasonably account for the contrasting results. First, in the present experiment the reaction signal S2 had two alternatives, left light or right light, although the response to both was a plantar flexion of the right foot. One could argue that preparation in general cannot be as intense in such a situation since it has been shown that RTs may be lengthened, when the number of different signals to which the same response has to be made, is increased (Teichner & Krebs, 1974). Consequently, a weakening of the relative inhibition in the involved leg could be expected. In addition, the compatibility of a particular stimulus and its response might be of importance here. It means that responding with the right foot to a stimulus at the right side of the stimulus display, or responding toward the source of stimulation as it was called by Simon (1969), would be easier than responding with the right foot to a stimulus located at the left. This mechanism could, again, have caused the level of preparation and the differential effect during the foreperiod to decrease. But the absence of a difference in response speed or error rate following the left or right S2 in the simple RT task makes this explanation unlikely. The former argument however, saying that an increase in the number of response signals renders motor preparation less intense, cannot be ruled out. To assess the level of motor preparation in different studies one could com-

pare RTs. In the case of the Brunia et al. (1982) study and the present experiment, such a comparison is hampered by differences with regard to (a) response manipulandum characteristics and (b) points in time at which reflexes were evoked: For RTs have been shown to become shorter as the reflex is positioned nearer the response signal (Michie, Clarke, Sinden, & Glue, 1976).

The second explanation for our failure to observe a clear difference between the involved and non-involved legs in the simple RT task is to be found in the instruction given to and the strategy adopted by the subjects during preparation. The instruction to the subjects in the RT conditions of the present experiment was to respond as fast as possible but to remain relaxed and not tense any muscle at the same time. The importance of minimizing the number of errors was stressed, while the limit above which responses were considered too late was rather high. From our EMG data in all three conditions, it is evident that subjects at least succeeded in relaxing the muscles involved as agonists in the response. It is conceivable that when speed of response rather than accuracy is stressed in the subject's performance another strategy is adopted in which increasing the tonic contraction level of the agonist muscle during preparation may assist in producing faster RTs (Sanders, 1980). The question whether such an increase in activation of the agonist can in fact be held responsible for the differential effect observed in former studies has to remain unanswered. The effect of agonist muscle tension, however, was clearly demonstrated by Haagh et al. (1983) who found that the instruction to tense the involved soleus muscle during unilateral response preparation caused the reflex difference between the two legs to increase at the moment of S2 onset. Instructing the subjects to relax both soleus muscles caused the differential effect to almost disappear and the RTs to grow larger. Similar results, as yet unpublished, were obtained in our laboratory with regard to reflexes evoked during the ISI. Since it has been shown that subjects, when encouraged to prepare for a fast response, often tense the agonist muscle unintentionally and without realizing that they do so (Burke, McKeon, Skuse, & Westerman, 1980; Haagh et al., 1984), this seems to be the most plausible explanation for the occurrence of a differential effect.

In this experiment we observed a reflex increase during motor preparation, while background EMG was unaffected. This finding is in agreement with data collected outside a warned reaction time paradigm by Gottlieb and Agarwal (1979). They reported an increase in the first component of the stretch evoked EMG response in the calf muscle when subjects were instructed to resist rotation of the ankle by which the reflex response was caused. Background EMG of the agonist muscle showed no changes in their study. In a recent experiment by Wolpaw, Seegal, and O'Keefe (1983), it was shown that monkeys are able to selectively increase the amplitude of the earliest segmental response to sudden biceps stretch without any accompanying change in agonist, antagonist, or synergist muscle activity. So it appears that a modulation of reflex gain is possible that is not due to changes in background activity of task related muscles.

Furthermore, there is evidence that when the skeletomotor system is relaxed there is no resting fusimotor tone (Burke, Hagbarth, & Wallin, 1980). In subjects at rest, fluctuations of monosynaptic reflexes in the soleus muscle were observed during a foreperiod, while no change in activity could be recorded in Ia afferents from the same muscle (Gerilovsky, Struppler, Altmann, & Velho, 1983). Although we did not record EMG activity in other than the triceps surae muscles, EMG activity in related muscles cannot be expected to have been very strong. It seems plausible, therefore, that the reflex changes recorded in the present experiment reflect facilitating activity in descending central pathways.

In summary, it appears that the Achilles tendon reflex is a measure sensitive to the facilitating effects of both stimulus presentation and the motor preparatory process. Preparing for a task which is non-motor in character does not necessarily give rise to such changes. The increase of reflex amplitudes observed in our experiment probably reflects a subliminal increase in motoneuron excitability, since it is not accompanied by changes in background EMG activity. During such a state of muscular relaxation, however, the amount of (limb-) selectivity in the preparatory process does not become manifest in the T reflex time course. This is contrary to what could be expected from earlier experiments. More research needs to be done to assess the exact influence of muscle tension on the T reflex.

In the present experiment, it is only after S2 when reflex amplitudes may be contaminated by the voluntary EMG response that a difference between the choice and simple RT tasks becomes evident on both the physiological and the behavioral level.

NOTE

1. Part of the data to be discussed here has previously been presented in abstract form at the tenth annual Scientific Meeting of the Psychophysiology Society, London, 15th–17th December 1982.

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Appendix 4.

Motor preparation and the Achilles tendon reflex: the role of background muscle tension

MOTOR PREPARATION AND THE ACHILLES TENDON REFLEX: THE ROLE OF BACKGROUND MUSCLE TENSION

Accepted for publication 5 June 1986

The effects of instructed tension or relaxation of the soleus muscles on the amplitude of the Achilles tendon reflex were investigated. Reflexes were evoked during the foreperiod of a warned reaction time experiment with a plantar flexion of the right foot serving as the response, and during isometric contractions of the right soleus muscle at different low levels of tension. The tension levels were related to the subject's maximal voluntary contraction force. The results were comparable in the two tasks. When background muscle tension was present in the right leg the reflexes in that leg were depressed, whereas in the contralateral leg reflexes were increased. This difference in amplitude was roughly proportional to the amount of tension and independent of whether the antagonist muscle was also activated during the contraction. It was argued that the differential reflex effect found in the two soleus muscles during motor preparation need not be a reflection of a selective neural inhibition. It could also be explained by a reduced effectiveness of the tendon tap in stretching the muscle, due to stiffening of the muscle during contraction. It was concluded that during motor preparation, only reflex changes recorded in the absence of muscle tension can be considered reflections of subliminal changes in spinal reactivity.

1. Introduction

Spinal reflex mechanisms can be preset by nervous activity from the brain, related to preparation for action (Hammond, 1956; Paillard, 1955).

The Achilles tendon (T) reflex, for instance, has been studied extensively during the fixed foreperiod of warned reaction time (RT) experiments. It was shown that during the foreperiod, reflex amplitudes were affected differentially, according to whether the triceps surae muscle was involved or not involved in the impending movement (Brunia, 1983; Brunia, Scheirs, & Haagh, 1982; Requin, 1969; Requin & Paillard, 1971). Reflexes evoked in the noninvolved muscle were found to be increased, while those evoked in the involved muscle decreased below baseline or were unaffected. A dual mechanism was proposed, first by Requin and Paillard (1971), to account for these results: a

general facilitation acting on both involved and noninvolved spinal motor structures and an inhibitory mechanism, presumably presynaptic, acting on the involved motor structures only.

Spinal reflexes were considered to be sensitive to neuronal changes even subliminal to the discharge of motoneurons (Paillard, 1955). Thus, these reflexes have been employed to reveal aspects of the preparatory process which, as was believed, could not become evident from studying background electromyographic activity (EMG) alone (Brunia, 1984; Requin, Bonnet, & Semjen, 1977). In a recent RT experiment it was shown that in relaxed subjects, reflexes can be modulated without concomitant changes in the agonist surface EMG (Scheirs & Brunia, 1985). However, the influence of agonist muscle tension on the T reflex has long been recognized. An increase in isometric muscle tension leads to decreased reflex amplitudes (Paillard, 1955), or to increased amplitudes at low tension levels followed by a decrease at higher levels (Ott & Gassel, 1969).

There is evidence that during preparation to move, subjects sometimes tense agonist or antagonist muscles, even without an explicit instruction to do so (Burke, McKeon, Skuse, & Westerman, 1980; Haagh & Brunia, 1984). This could provide a serious difficulty to the interpretation of reflex changes during a foreperiod. Since during muscle contraction which is almost isometric in the type of experiments considered here, minor changes in leg position and in mechanical properties of the muscle might also occur, an interpretation in terms of facilitatory and inhibitory neural influences acting on the reflex arc could be hazardous.

The aims of the experiments reported here were to: (1) Demonstrate the effects of muscle tension on the T reflex, both in and outside a warned RT task; and (2) offer an alternative explanation for the differential reflex effect that was observed during the foreperiod in former studies.

2. Experiment 1

In experiment 1, the effects of instructed muscle tension on T reflexes evoked during the fixed foreperiod of a simple RT task were investigated. As aspects of the motor preparatory process are thought to be most clearly revealed shortly before the movement, although not exclusively (Scheirs & Brunia, 1982), reflexes were evoked only during the later part of the foreperiod.

2.1. Method

2.1.1. Subjects and apparatus. Twenty righthanded subjects, 12 males and 8 females, were paid to participate in the experiment. Most of them were

students of psychology. Their age varied from 18 to 34 years (mean age = 22.9 years).

Subjects were seated in a comfortable chair, which was placed in a dimly illuminated and electrically shielded chamber. The subject's feet were strapped to movable footplates with microswitches underneath for the recording of reaction times. The knees and ankles were positioned in approximately 120 and 90° of flexion, respectively. Submaximal T reflexes were elicited by means of two Brüel and Kjaer 4809 vibration exciters, which were directed at a right angle to the Achilles tendon at the level of the medial malleolus. The vibration exciters were triggered by a 9 ms pulse of constant amplitude, produced by a Brüel and Kjaer 2706 power amplifier. A buzzer was used as a warning signal (S1). Its intensity was 80 dB (A) and its duration 100 ms. A 2900-Hz tone produced by a Sonalert (75 dB (A), 1 s duration) served as an RT feed-back signal, and the illumination of a circular red LED display was used as a reaction signal (S2).

The electromyographic responses were recorded via two Ag/AgCl surface electrodes attached on the distal part of each soleus muscle, the centres of the electrodes being about 5 cm apart. The signals were differentially amplified (−3dB bandwidth: 3.8–520 Hz; 31 dB and 13.5 dB down/octave respectively) and stored on magnetic tape by means of an instrumentation recorder (Hewlett and Packard 3968 A; flat frequency response within ±1 dB: 0–312 Hz). EMG feedback to the subject was provided by feeding the rectified and low pass filtered (−3dB : 0.2 Hz) background EMG of the right soleus muscle into the voltage controlled input of a IEC F34 function generator. The square wave output of this generator was fed into a speaker, which resulted in clearly audible clicks rapidly increasing in rate during muscle contraction.

2.1.2. Procedure. The experiment consisted of two conditions and was run according to a within-subjects design. The order of the conditions was counterbalanced between subjects. The conditions consisted of 56 trials each. On each trial, presentation of S1 was followed by S2 after a delay of 4 s. A rapid response (plantar flexion of the right foot) was required to S2. The 4-s foreperiods were interspersed with inter-trial-intervals (ITIs) of 16 s.

Reflexes were elicited once during each foreperiod, at one out of eight different latencies: At 2, 2.5, 3, 3.5, 3.7, 3.8, 3.9, or 4 s after S1 onset. The order of these latencies varied pseudorandomly, in such a way that each latency occurred seven times. A control reflex was elicited once during each ITI at 6, 8 or 10 s after S2 onset, the order of these latencies also being chosen pseudorandomly. Reflexes were always evoked simultaneously in both legs. Care was taken to elicit reflexes of about the same amplitude at both sides.

Background EMG from both soleus muscles was recorded continuously. RTs were measured to the nearest ms, printed on paper and shown to the subject by means of a four digit display immediately following the response.

Reactions with latencies shorter than 150 ms or longer than 400 ms were followed by auditory feedback. Feedback informed the subjects that their RTs were not within the acceptable range.

In one condition (tensed condition) subjects were instructed to selectively tense their right, response-involved soleus muscle during the foreperiod in order to attain RTs as short as possible. They had to relax again after the response had been given. In the other condition (relaxed condition), subjects were instructed to relax all muscles including the involved soleus muscle, even if this resulted in longer RTs.

Prior to the experimental session, all subjects received a training session in which they practiced tensing and relaxing their muscles by means of auditory EMG feedback. During the experimental session EMG feedback was disconnected. Left and right soleus EMG continued to be monitored by the experimenter, in order to be able to detect gross bodily movement.

2.1.3. Data analysis. EMG and reflex responses were digitized off line (sample frequency: 1024 Hz). Trials containing premature or late responses as well as those containing movement artifact were discarded from further analysis. Peak-to-peak amplitudes of reflexes were measured and individual averages were calculated in each leg and at each reflex latency. These averages were then expressed as percentages of the corresponding mean control reflex amplitude for each subject.

After digitizing, the absolute EMG values obtained during the foreperiod were summated over successive 100 msec epochs and expressed as percentages of the mean summated EMG calculated over the twelfth second of each ITI. EMG was not analyzed during an interval of 500 ms following the reflex eliciting stimulus. This was done to avoid a possible contamination of the background EMG trace by reflex potentials.

The EMG and reflex percentage scores, averaged over subjects, were used for the illustrations. The individual EMG percentages, reduced to averages calculated over 5 successive epochs of 100 ms, as well as the individual T reflex percentages were used in the statistical testing procedures.

2.2. Results and discussion

In the tensed condition, subjects tensed their right soleus muscle to attain faster RTs (mean RT = 249 ms). This RT was significantly faster than the RT in the relaxed condition (mean RT = 269 ms; $t(19) = 4.36$, $p < 0.01$). The number of premature and late responses did not differ statistically between conditions (errors tensed condition: 5.2%; relaxed condition: 3.9%).

Fig. 1 indicates that in the tensed condition, reflexes in the left leg were increased during the later part of the foreperiod, while those in the right leg were decreased below baseline. An analysis of variance (ANOVA) with

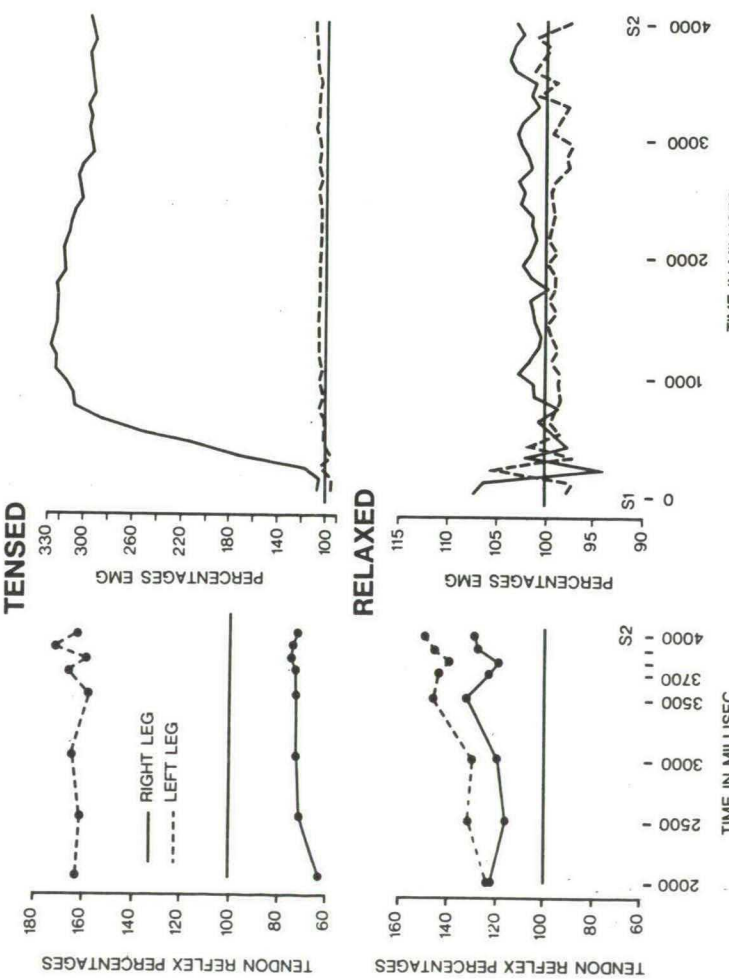

Fig. 1. Achilles tendon reflexes and surface EMG of the soleus muscles during instructed tension and relaxation of the right soleus in a reaction time task. Reflexes were evoked during the later part of the 4 sec foreperiod only, while EMG was recorded continuously. The required response was a plantar flexion of the right foot. Amplitudes are expressed as percentages, relative to the mean control reflex and EMG level (control = 100%).

Recording Side and Reflex Latency as within-subjects factors showed that the difference between the two legs was significant (main effect of Recording Side: $F(1/19) = 36.28$, $p < 0.01$). In the relaxed condition, the difference between the left and the right leg just failed to reach significance (main effect of Recording Side: $F(1/19) = 3.20$, $p < 0.10$), and there was a change of reflex amplitudes over time (main effect of Reflex Latency: $F(7/133) = 3.05$, $p < 0.01$). Furthermore, the reflex averages in this condition were found to be significantly above baseline both in the left and in the right leg ($t(19) > 2.40$, $p < 0.05$ for reflexes at all latencies).

It appears from fig. 1 that instructed muscle tension greatly influenced the differential reflex effect as described in the introduction, the effect being largest when the involved muscle was tensed.

In the tensed condition, there was a small irradiation of voluntary motor activity to the contralateral soleus muscle. This phenomenon has been found to occur during even minor contractions of foot and finger muscles (Cernacek, 1961; Davis, 1942). In the relaxed condition, a slight EMG increase was apparent in the right soleus muscle. It is doubtful whether these small increases in muscle tension contributed substantially to the reflex results, as in general the absolute EMG amplitudes recorded in relaxed muscles were not larger than 2 or 3 μV and thus were close to noise level.

In summary, it appears that the selective setting of spinal motor structures prior to movement which has often been observed (Brunia, 1983; Brunia et al., 1982; Requin, 1969; Requin & Paillard, 1971) can at least in part be explained by agonist muscle tension. It seems, therefore, that an interpretation of reflex changes as reflecting primarily neural influences acting on the reflex arc, be it post- or presynaptically, is not the most parsimonious one.

3. Experiment 2

Experiment 2 investigated the effects of different degrees of muscle tension on T reflexes outside an RT task.

Tension of a muscle can be measured by analyzing force output or, indirectly, by taking the mean rectified or integrated surface EMG. The surface EMG is a complex function of rate of firing, recruitment and amount of synchronization of motor units. Furthermore, a certain level of force can be achieved in several ways, by different patterns of muscles contracting together. It is not surprising, therefore, that there has been considerable debate concerning the linearity of the relationship between force and EMG. Much of this controversy, however, seems to be due to differences in experimental procedure (Moritani & deVries, 1978; Metral & Cassar, 1981). Whatever the exact nature of this relationship, there is agreement that when fatigue is avoided, the integrated EMG during isometric contractions is an effective indirect measure

of muscle force (Bouisset, 1973; Hof, 1984). Thus, we will treat tension, force and integrated EMG of a muscle as equivalent concepts.

In order to allow for interindividual comparability of different tension levels in this experiment, the induced tension was expressed as a percentage of the tension the subjects can develop during a maximal voluntary contraction (MVC). Although reproducibility of maximal force on different occasions may be low in leg muscles (Hof, 1984), it has been shown that maximal plantar flexor strength can be reached during relatively short contractions (lasting a few seconds) (Kamen, 1983) and that, in the human soleus muscle, all motor units can be fully activated by voluntary effort (Bellemare, Woods, Johansson, & Bigland-Ritchie, 1983).

We attempted in the present experiment to induce very low levels of tension, which might be compared to the tension levels employed during RT tasks by some subjects who have received no explicit instruction to do so. Such low tension levels may be considered to cause no fatigue. It was shown that tensions in forearm muscles below 10% MVC could be held indefinitely and without any signs of fatigue in the EMG (Petrofsky, 1980). Tensions were induced in the right leg only. No attempts were made to counterbalance leg tensed (left or right) across subjects, since former studies had not revealed the contribution of a dominance factor to the reflex time course (Brunia, 1983; Brunia et al., 1982).

3.1. Method

3.1.1. Subjects and apparatus. Fourteen righthanded subjects, 6 males and 8 females, were paid to participate. Their age varied from 18 to 30 years (mean age = 23.5 years).

Positioning of the subjects, evocation of reflexes and recording of the EMG signals were the same as in experiment 1. In addition, tibialis anterior EMG was recorded by placing two surface electrodes over the bellies of the muscles with the centres about 5 cm apart. Stimuli and feedback were not presented, except for the presentation of the right soleus EMG that was rectified and summated over 100-ms or 1-s epochs and continuously shown to the subject via an oscilloscope screen.

3.1.2. Procedure. All subjects took part in one experimental session. They were asked to execute a MVC with the right plantar flexors on 5 or 6 separate trials, while their feet were fixed. Each trial was approximately 3 s in duration with a 1 min rest between trials. The highest EMG value attained, as read from the oscilloscope by the experimenter, was taken as the MVC value.

Then, after an initial rest period, subjects were instructed to tense their right soleus muscle at 2%, 1%, 0.5% or 0.25% of MVC by means of the oscilloscope signal. The various force levels were applied in descending order,

with periods of about 5 min between. During tension of the right soleus muscle, which was maintained for about 90 s at each of the levels, subjects had to relax all other muscles. After the descending series had been completed, a second rest period was introduced. Left and right soleus EMG were monitored by the experimenter. All subjects performed during the two rest periods and during three or four force levels, either at 2%, 1% and 0.5% MVC or at 2%, 1%, 0.5% and 0.25%, depending on whether the very small 0.25% MVC level could be effectuated; the maximum force exerted by 6 subjects was too small to allow for a clearly discriminable and stable EMG trace at that particular level.

During the first and the second rest period and the near isometric contractions at the specified levels, 20 reflexes were evoked in both legs simultaneously, the consecutive reflexes being spaced by intervals of 4 s.

3.1.3. Data analysis. The analysis of reflex responses and EMG was similar to the data analysis in experiment 1. Data contaminated by gross movements were discarded, as were the data of one subject who was unable to relax the left soleus muscle. The reflexes evoked at a particular force level were split into two groups of ten successive reflexes, averaged per group and expressed as percentages of the first group of ten reflexes evoked during the first rest period. EMG values were obtained by rectifying and summating the EMG that was recorded during the third second of each interval between two consecutive reflexes. These EMG values were expressed as percentages in a way comparable to the reflex data, i.e. with the EMG values obtained during the first half of the first rest period as a reference.

3.2. Results and discussion

The averaged results of 13 subjects are shown in fig. 2. It appears that when the right soleus muscle was tensed, the antagonist muscle, the m. tibialis anterior, was coactivated in a roughly proportional manner.

Of the 13 subjects, 9 behaved in this way, whereas only 4 were able to tense the agonist muscle selectively. The results of this small subgroup are presented in fig. 3. It has to be noted that the increased tibialis anterior activity during the weakest contraction in this group was due to the results of one subject.

To test whether the left and right leg data differed significantly, an ANOVA was carried out on the reflex data of the complete group of subjects, with Force Level and Recording Side as within-subjects factors. There was a significant main effect of Force Level ($F(5/52) = 3.34$, $p < 0.01$) and Recording Side ($F(1/12) = 16.95$, $p < 0.01$). The interaction effect was also significant ($F(5/52) = 8.92$, $p < 0.01$). Contrasts among treatment means according to Scheffé revealed that the left/right differences were significant only in the 2% and 1% MVC conditions (critical s = 79.62 and 82.88 respectively; contrast values = 122.6 and 104.5 respectively, $p < 0.05$). The increasing reflex values

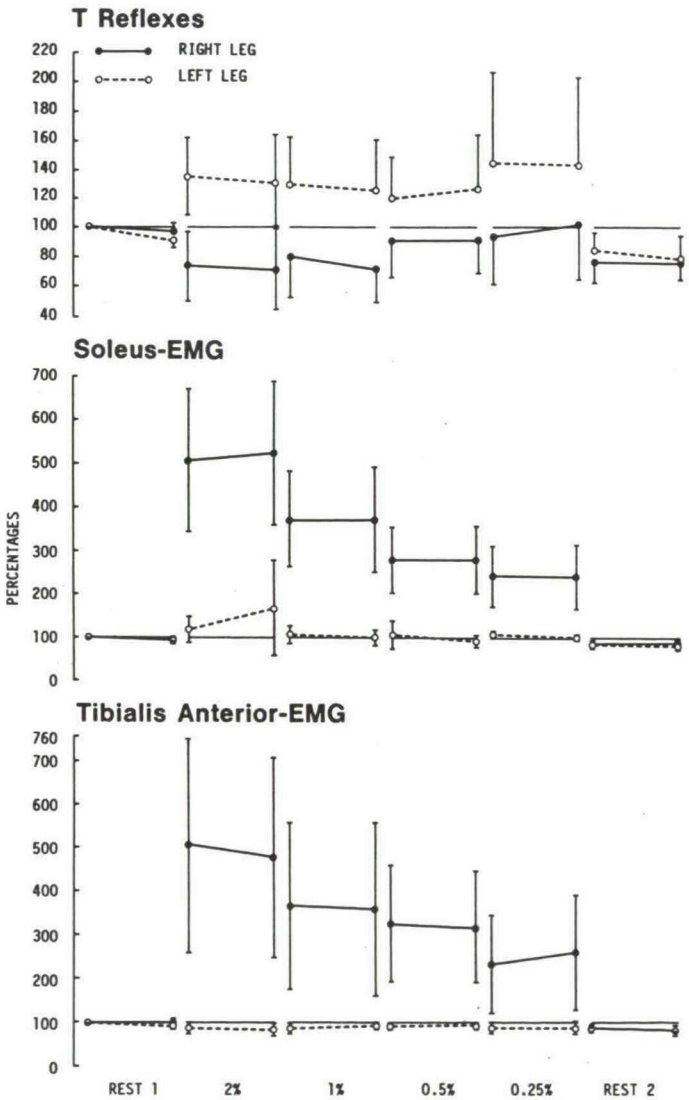

Fig. 2. Achilles tendon reflexes and surface EMG during rest and during the instructed tension of the right soleus muscle at different levels of tension. The percentages along the abscissa indicate tension levels relative to maximal voluntary force as assessed by integrated EMG. Each data point represents the average of 10 consecutive trials. Amplitudes are expressed as percentages, relative to the values obtained during the first half of the first rest period. The vertical lines indicate 95% confidence intervals. The data are from the total group of 13 subjects.

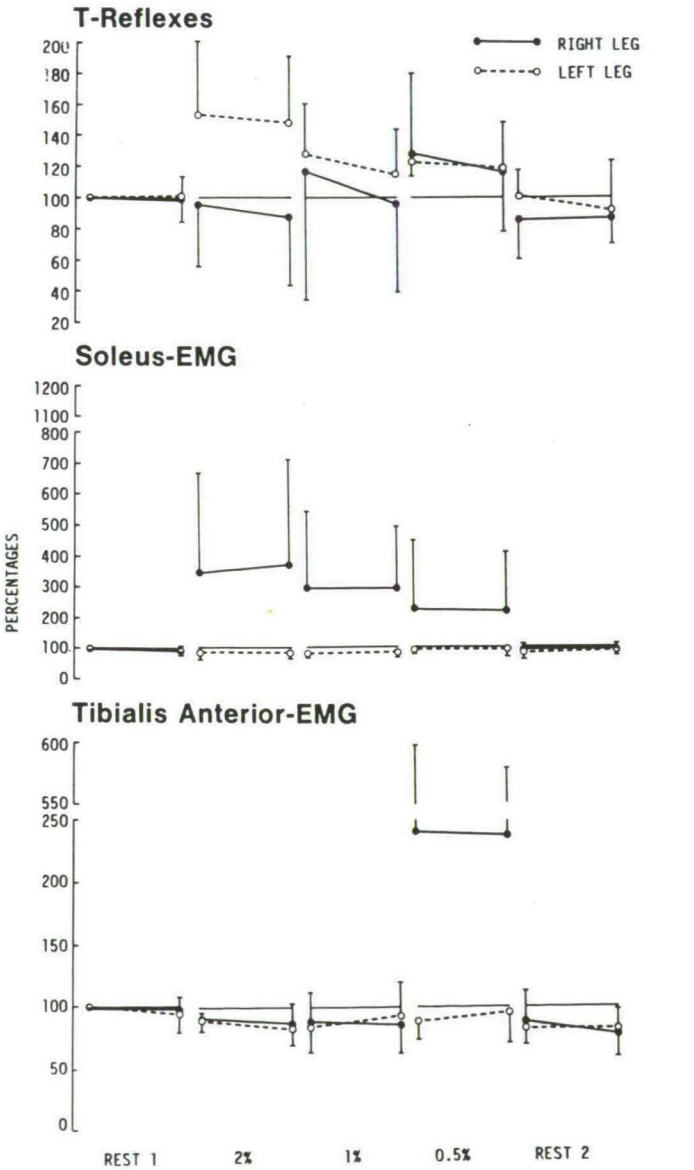

Fig. 3. Data as in fig. 2, from a subgroup of 4 subjects who did not coactivate the tibialis anterior muscle during contraction of soleus.

in the right leg as tension decreased from 2% MVC to 0.25% MVC, which was seen in fig. 2, did not reach statistical significance. Neither was there a significant difference among the left leg values at these tension levels.

Figs. 2 and 3 indicate that at the highest level of unilateral muscle tension and regardless of whether the antagonist muscle was also activated, reflexes in the contralateral leg were increased while those in the ipsilateral leg were depressed. This interlimb difference tended to grow smaller as the right leg tension decreased. The effect was probably due to the gradual increase of the reflexes in the right leg, as the reflexes in the left leg remained above baseline at all force levels. This is best illustrated in the four subject subgroup (fig. 3), where the differential effect disappeared at the lowest force level. The data from this subgroup also indicate that the tibialis anterior activity recorded in the majority of the subjects cannot be explained by cross-talk from soleus.

Table 1
Intrasubject variability (coefficients of variation) of the reflexes and EMG activity shown in fig. 2. (the numbers in the column headings refer to the first and second half of the recording periods)

	Left leg		Right leg	
	1	2	1	2
Rest 1				
Reflexes	0.286	0.218	0.204	0.199
soleus EMG	0.297	0.243	0.223	0.185
Tibialis EMG	0.173	0.159	0.156	0.186
2%				
Reflexes	0.269	0.233	0.288	0.237
Soleus EMG	0.206	0.150	0.082	0.071
Tibialis EMG	0.175	0.124	0.110	0.129
1%				
Reflexes	0.228	0.224	0.208	0.250
Soleus EMG	0.137	0.138	0.082	0.073
Tibialis EMG	0.130	0.135	0.106	0.104
0.5%				
Reflexes	0.258	0.208	0.207	0.217
Soleus EMG	0.142	0.159	0.078	0.090
Tibialis EMG	0.137	0.122	0.104	0.128
0.25%				
Reflexes	0.216	0.204	0.225	0.226
Soleus EMG	0.123	0.097	0.106	0.081
Tibialis EMG	0.111	0.170	0.124	0.090
Rest 2				
Reflexes	0.295	0.248	0.247	0.235
Soleus EMG	0.137	0.118	0.134	0.141
Tibialis EMG	0.123	0.116	0.156	0.122

The averaged data show a co-contraction of antagonist muscles around the ankle joint. Although reciprocal inhibition is a basic mechanism in motor control, such a co-contraction is not exceptional (Tanaka, 1983). It is frequently observed during inexperienced motor performance and also in the presence of rapid perturbing forces which may destabilize the joint (Humphrey & Reed, 1983). Both conditions seem to be satisfied in the present experiment, with the subjects receiving little training and the tendon tap serving as the perturbing stimulus.

The confidence intervals displayed in figs. 2 and 3 are based on individual averages. To obtain a measure of intra-individual variability, coefficients of variation were calculated for each of the 13 subjects separately and averaged over subjects. The resulting mean values are given in table 1. It can be seen that reflex variability remained almost constant across tension levels. During contraction of the right soleus muscle, however, variability of the EMG recorded from that muscle decreased. Variability of the tibialis anterior EMG, on the other hand, was hardly affected by tension. These results suggest that co-contraction is not a consistent phenomenon, neither between nor within subjects.

4. General discussion

Our experiments show that even a slight tension of one of the two soleus muscles influences the amplitude of the tendon jerk on both the ipsilateral and the contralateral side. The amplitudes are increased in the non-activated muscle and decreased in the activated muscle, while the latter decrease tends to grow smaller with decreasing tension. The most important result appears to be that during preparation of a motor response in the tensed condition, a reflex pattern emerges that is highly comparable to the pattern observed during the mere task of maintaining a certain level of tension (i.e. the higher levels in our range). The reflex pattern observed during motor preparation in the relaxed state has no clear counterpart in the tension maintaining task, although it resembles the lowest force level in the four subject subgroup; the trend in the data shown in fig. 1 predicts such a pattern to occur in the total group of subjects at tension levels even less than 0.25% MVC. A reflex increase in the left soleus muscle, which was uninvolved in the impending movement or in the maintaining of tension, is seen throughout the present experiments. It has also been a consistent finding in former studies where T reflexes were evoked bilaterally; the increase was found both when background EMG activity was absent (Scheirs & Brunia, 1985) and when EMG was not recorded (Brunia, 1983; Brunia et al., 1982; Requin, 1969; Requin & Paillard, 1971). Up to now this increase has been found only when subjects engage in a motor task; that is, when they prepare for a fast limb movement or

tense the contralateral muscle isometrically. It has not been found during anticipation of a significant stimulus (Scheirs & Brunia, 1985).

We suggest, therefore, that this reflex increase is related to the instantaneous or anticipated performance of a motor act, and that it is a true reflection of a subliminal change in spinal excitability. The increase seems to be a result of central rather than peripheral influences acting on the reflex arc, as muscle spindle sensitivity was shown not to change when tendon jerks of various amplitude were evoked in the relaxed human soleus muscle (Burke, McKeon, & Skuse, 1981). The site of central action within the reflex circuit remains unknown. It could be directly on the alpha motoneurons or, since the tendon jerk is probably composed also of oligosynaptic pathways (Burke, Gandevia & McKeon, 1984), on spinal interneurons. The action could also be exerted by presynaptic influences affecting the Ia afferent terminals.

The relative depression of the reflexes in the right leg in the present experiments, both in and outside the warned RT task, was shown to occur secondary to background muscle tension. In warned RT studies in which muscle tension was clearly prevented (experiment 1; Scheirs & Brunia, 1985), such a decrease was absent or small. Until recently the mechanism of presynaptic inhibition was frequently advocated as the cause of this depression (Bonnet, Requin, & Semjen, 1981; Brunia, 1983). Based on combined recordings of reflexes and EMG, however, some alternative explanations were proposed by Haagh, Spoeltman, Scheirs, and Brunia (1983). First, they pointed to the possibility of a postsynaptic inhibitory mechanism. But since such a mechanism would cause the background EMG and the reflex output to vary in the same direction, this explanation is not very plausible with regard to the present data. The explanations that remain are: (a) Occlusion of the reflex with motor units that are voluntarily activated or that are in the refractory phase (Ott & Gassel, 1969); and (b) a decreased effectiveness of the tendon tap as a result of a small change in leg position or of muscle stiffening during the contraction. In the human soleus muscle, the modulation of force is accomplished primarily by motor unit recruitment (Bellemare et al., 1983). When the recruitment mechanism is active, muscle stiffness has been shown to vary according to the exerted force (Houk & Rymer, 1981).

We propose, without denying that other processes could be active at the same time, that the relevance of the second explanation has been underestimated. An increased muscle stiffness can reduce the impact of the reflex eliciting stimulus and thus contribute to a decrease in reflex amplitudes. Support for this proposition is provided by the fact that isometric muscle tension causes two other spinal reflexes, the electrically elicited Hoffmann reflex and the first component of the stretch reflex in soleus, to increase within a wide range of tension levels (Gottlieb, Agarwal, & Stark, 1970; Kearny & Chan, 1982). In contrast, the tendon jerk is depressed. These three types of reflexes are not simple equivalents. Evidence has accumulated that the tendon

jerk and the Hoffmann reflex, for instance, differ with respect to their afferent volleys (Birnbaum & Ashby, 1982; Gassel & Diamantopoulos, 1966). Most differences, however, seem to be directly related to the nature of the reflex eliciting stimulus (i.e. electrical stimulation versus stretch of the muscle), rather than to the neural circuitry that is involved (Burke, 1983). The eliciting stimulus in case of the Hoffmann reflex is stimulation of the posterior tibial nerve by a constant electrical current. In case of a stretch reflex the eliciting stimulus is rotation of the ankle over a predetermined angle. It is conceivable that the effectiveness of both stimuli is affected less by a change in muscle stiffness than is the effectiveness of a tendon tap.

We conclude from this that T reflexes evoked during the foreperiod of RT experiments are reliable estimators of spinal reactivity only when background muscle tension is absent. If tension is present, a relative reflex depression is likely to result that can be explained by a reduced effectiveness of the reflex eliciting stimulus. Whether a neural inhibition is still active in such a situation remains open to question. If our alternative explanation proves to be valid, the motor preparatory process is not characterized by a selective inhibition but by facilitation, which may be generalized or selective depending on the instructions given to the subject. The alternative view says that, when the instruction is to respond quickly but not to tense any muscles, preparation is characterized by a subliminal increase in motor output that is present at all levels of the spinal cord; when the instruction is to respond as fast as possible, the increase in activation is most prominent in the motor structures that are involved in response execution. Here, the activation is supra-threshold. Activation patterns such as these may not be unique to motor preparation either: Tensing the muscle outside a reaction time task and the instruction to prepare for a movement may give rise to similar changes in EMG and reflexes, as our experiments have shown.

An interesting aim for future research would be to compare the time courses of reflexes evoked by stretch and by tendon taps under varying degrees of muscle tension. However, it is unlikely that recordings at the surface of the human body can solve the question as to the role of peripheral versus neuronal factors in reflex control. Direct neurophysiological evidence, obtained from man or animal, is needed to shed more light on the basic mechanisms which are involved in reflex modification.

Acknowledgements

This work was supported by the Tilburg Institute of Advanced Studies (TIAS). Part of the experiments grew out of discussions with Ton van Boxtel and Stephan Haagh. Jan Pijnenburg prepared the figures.

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Stellingen behorend bij het proefschrift van J.G.M. Scheirs:
Motor Preparatory Processes Recorded in the Leg of Man

1. De voorbereiding op een motorische respons wordt bij de mens gekenmerkt door een toegenomen neurale, faciliterende aktiviteit.

2. Indien bij psychofysiologisch onderzoek maten worden geregistreerd waarvan de fysiologische werkingsmechanismen niet bekend zijn, dan is de waarde van dat onderzoek voor de psychologie beperkt.

3. Van reflex-veranderingen tijdens taak-belasting zijn de werkingsmechanismen niet bekend.

4. De in wetenschappelijk opzicht weinig efficiënte en in menselijk opzicht frustrerende praktijk om wetenschappelijke onderzoekers slechts een tijdelijk dienstverband aan te bieden, dient te worden bestreden door er in proefschriften die desondanks tot stand zijn gekomen stellingen over op te nemen.

5. De konklusie van Bonnet: "La préparation d'un mouvement balistique s'exprime par une inhibition présynaptique des afférences fusoriales du muscle soléaire impliqué dans la réponse volontaire.", steunt op onvoldoende bewijsmateriaal. (M. Bonnet, Etude réflexologique chez l'homme de la préparation au mouvement. Thèse de doctorat, Marseille, 1984, p.102).

6. Resultaten uit de experimentele psychologie bieden voldoende aanknopingspunten om te veronderstellen dat het aantal ongevallen bij bewaakte spoorwegovergangen kan worden verminderd door niet alleen een rood licht te laten funktioneren als stopsignaal, maar ook een groen licht als teken dat de doorgang veilig is.

7. Daar de introduktie van de windmolen in West-Europa in de 12-de eeuw niet te verklaren valt op grond van een geleidelijke ontwikkeling uit de inheemse watermolen of de windmolen uit Voor-Azië, lijkt de konklusie gewettigd dat het idee ontsproten is aan het brein van een geniaal individu.

8. De Rijks-monumentenzorg in Nederland verdient het predikaat "zorg" niet, daar het beleid dat gevoerd wordt hoofdzakelijk gericht is op het op aanvraag ter beschikking stellen van (te weinig) geld.

9. "We are too vain. We think we are the summit of history." (M. Bishop, The Penguin Book of Middle Ages, 1971).

10. De ontwikkelingen in het Nederlandse universitaire bedrijf geven aanleiding tot de gedachte, dat bij een toenemend aantal proefschriften het lachen niet beperkt zal hoeven te blijven tot de stellingen.